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Cenomanian brachiopods from the Lower Chalk of Britain and northern Europe

E. F. Owen

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E. F. Owen

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

A brief history of Cretaceous brachiopod research over the past 120 years is followed by an account of the distribution of the major brachiopod-bearing outcrops of Lower Chalk (Cenomanian) age in Britain and northern Europe. The apparent control that some substrates had in the distribution of faunal assemblages is described, and also their relationship to changes in lithology. The more important Cenomanian brachiopod taxa are described and updated, and several new stratigraphically important taxa are proposed, including the new terebratulacean genus *Ovatathyris*.

New species of Rhynchonellaceae are: *Cyclothyris punfieldensis*, *C. formosa*, *C. juigneti*, *Burrirhynchia devonia*, *Orbirhynchia wilmingtonensis* and *O. boussensis*. New species of Terebratulaceae are: *Ovatathyris potternensis*, *Boubeithyris diploplicata*, *Rectithyris wrightorum*, *Tropeothyris vectis*, *Moutonithyris anglia*, *Terebratulina imbricata* and *T. protostriatula*, the latter *pro* the '*Terebratula striatula* Mantell' of authors, *non* Mantell. *Terebratulina etheridgei* nom. nov. is proposed to replace *T. triangularis* Etheridge, *non* Tate. The new subspecies *Dereta pectita ballardensis* is also proposed.

Lectotypes are selected of *Lingula subovalis* Davidson, *Sellithyris phaseolina* (Valenciennes, *in* Lamarck) and *Concinnithyris subundata* (J. Sowerby). Neotypes are designated for *Sellithyris tornacensis* (d'Archiac) and *Terebratulina nodulosa* Etheridge.

Introduction

There are few major works on Cretaceous brachiopods beyond those of northern Europe and the United Kingdom and most of the important works have been confined to comparatively sparse local faunas. The following account, therefore, deals mainly with British, French and German species, except for a few forms described from outside this area.

It is important to note that, while the work here is chiefly concerned with species of Cenomanian age, it has been necessary to include a brief mention of some Albian species. These are, in the main, long-ranging forms, such as those from the Upper Greensand, or facies-controlled species of Cenomanian aspect such as occur in the Shenley Limestone, Leighton Buzzard, Bedfordshire, which are of undoubted Lower Albian age.

Great Britain

In Britain many Cretaceous brachiopods were named and described for the first time by James Sowerby (1815–18), and later his son, James de Carle Sowerby (1826–45), usually under the single generic name *Terebratula*. Cenomanian species described by the Sowerbys and considered to be valid include *T. lyra*, *T. pectita*, *T. ovata*, *T. obesa*, *T. mantelliana*, *T. obtusa*, *T. subundata and T. megatrema*. These and several other species have been revised here and provide most of the systematic part of this paper.

At the time that the Sowerbys were writing, very little information on stratigraphical age was available, and many specimens described and figured by them were accompanied by only a brief lithological description of the beds from which they came. Many of their species were based upon young stages of growth and, moreover, it is in some cases impossible to trace original material, especially since the Sowerby Collection, now in the British Museum (Natural History), is far from complete. Subsequent authors have often identified specimens by comparison with the Sowerby published illustrations alone and, consequently, many species which they have described are not always accurately recorded.

The work of the Sowerbys was largely superseded by the publication of Thomas Davidson's monographs (1852–54, 1874), which showed that he had a very profound comprehension of the phylum generally. His contribution to brachiopod taxonomy as a whole is still highly regarded and most of the Cretaceous species which he described are currently accepted.

Several decades elapsed before further work of significance was produced on British Cretaceous brachiopods. Sahni (1929) began a work on British Chalk Terebratulidae with discussion of previous research; he concluded '. . . it is doubtful if any value except historical attaches to the works cited above'. The works of Davidson and d'Orbigny were among those especially selected for critical discussion. Sahni ends his comments with the rather startling announcement that 'the confusion which has obtained in the nomenclature of the Chalk terebratulid species for over a hundred years has now been cleared.' It is a pity that Sahni was so critical,

because his own work is based almost entirely on poorly documented museum collections. He created a vast number of new names, largely based upon minor morphological variations. His attitude to the palaeontological opinions of previous workers contrasts strangely with his acceptance of museum labels as a key to stratigraphy, and his horizons are, at best, very vague. Where definite horizons are given, they are often very inaccurate, e.g. *Terebratula abrupta* Tate from the Upper Campanian of Northern Ireland is cited as Cenomanian. In fact it is very difficult to discuss Sahni's work, as any criticism is bound to be destructive. Nevertheless, his work does represent the first attempt to separate Cretaceous Terebratulidae into generic groups.

Pettitt's (1949, 1954) monograph on Chalk Rhynchonellidae dealt largely with species from Turonian to Lower Maastrichtian. This was an advance on the work of both Davidson and d'Orbigny in that it separated the two main generic groups in the Upper Cretaceous, represented by the new genera *Cretirhynchia* and *Orbirhynchia*. Pettitt's work was not complete and is not fully representative of the Chalk Rhynchonellidae, especially those of the Lower Chalk.

The most intensive study of the Cretaceous Terebratulidae in recent years has been by F. A. Middlemiss. His researches have concentrated largely on Lower Cretaceous species, although he has recently referred the Belgian Tourtia species *Terebratula tornacensis* d'Archiac to his genus *Sellithyris*, originally described from the Aptian (Middlemiss 1959). Middlemess has also shown that several genera and species thought to have been confined to the Lower Cretaceous in fact range up into the Upper Cretaceous.

A monographic study of the Terebratulacea from the Trias to Recent by G. A. Cooper (1983) includes a splendid series of hand-dissected specimens exposing brachidia and cardinalia. This unique work has greatly advanced our knowledge of the relationship of Cretaceous genera and species.

During the course of my own research, I have dealt with several genera which have similarly long stratigraphical ranges and appear well established in both Aptian and Cenomanian beds. One of these is the rhynchonellid genus *Cyclothyris* (Owen 1962). The dallinid *Kingena* Davidson was also reviewed (Owen 1970), and was shown to have a stratigraphical range from the Lower Albian to Upper Campanian, with two species in the Lower Chalk. Since then, a paper describing the morphological similarities in the internal structure of the Terebratellaceae was published (Owen 1977), in which possible evolutionary links between some genera and species were discussed.

France

The French Cretaceous was intensively studied towards the middle and end of the nineteenth century and many stratigraphical works appeared, which include original descriptions of brachiopod species. Brachiopods were described by Valenciennes in Lamarck's (1819) monograph of the fossils of France, which was partly contemporaneous with the work of the Sowerbys. Some of the taxa proposed by Valenciennes lacked stratigraphical details and were poorly illustrated. Among those which can be applied correctly to Cenomanian species are *Terebratula menardi*, *T. phaseolina*, *T. difformis* and *T. compressa*. Many points of confusion were cleared up by Davidson (1850), who revised and figured many of Valenciennes' species.

D'Archiac's (1847) description of the Belgian Tourtia species was followed by d'Orbigny's monumental work (1848–51). This included chapters on stratigraphical sequences and led to a scheme for the classification of the Cretaceous strata as a whole, which was published later in more detail (d'Orbigny 1852). In fact it is to d'Orbigny that we owe the stage name Cenomanian, it having been derived from the Roman name for Le Mans (Sarthe) where the beds are exposed.

The significance of brachiopod faunas in beds of the Lower Chalk was quickly realized by stratigraphers and many lists appeared of the species described by d'Orbigny. Barrois (1875, 1876) and Bigot (1893) were among those who acknowledged the importance of brachiopods at this stratigraphical level, especially where ammonites were scarce or absent. Recent contributions to the stratigraphy of Normandy and the Sarthe include the works of Kennedy & Hancock (1970), Juignet, Kennedy & Wright (1973), and Juignet & Kennedy (1976).

Germany

Early in the nineteenth century there was also considerable interest in the Cretaceous of Germany. Early German monographs included those of Schlotheim (1813, 1820) in which many Upper Cretaceous brachiopods were illustrated, including some of Cenomanian age. Later, Roemer (1840) described the brachiopod faunas of the Hilsconglomerat and the Essen Greensand.

Additional German species were erected by Quenstedt (1868–71), Geinitz (1872), Dames (1874), Diecke (1878) and Tiessen (1895). The one name which stands paramount among German workers, however, is Schloenbach (1867), whose concise and detailed descriptions were enhanced by good illustrations.

The early interest in the Cretaceous brachiopods was not maintained and, in keeping with most countries in western Europe, no notable works devoted to Cenomanian brachiopods have appeared from Germany since before the first World War.

Denmark

Although the Cenomanian is poorly exposed in Denmark, Ravn (1916, 1925) monographed the fauna from the Arnager Greensand of Bornholm. Two species of *Terebratella*, *T. kofoedi* and *T. bornholmensis*, were described as new and a third species was identified as *Terebratella beaumonti* (d'Archiac) (Ravn 1916). This species was referred to *Arenaciarcula* in the revision by Owen (1977: 236).

Distribution of some Cenomanian rocks

The Weald

Although there are many accounts of the geology of the Weald ranging from the works of Topley (1875) to the more detailed account of Jukes-Browne & Hill (1896, 1900–04), perhaps the most detailed descriptions of the Chalk of Sussex are those of Gaster (1929, 1937, 1939, 1944, 1951). He visited numerous localities where the Lower Chalk was well exposed in working quarries. Few are still available, but Gaster recorded brachiopods from most sections he visited, and his collection, presented to the British Museum (Natural History) in 1957, has been used during the course of the present study.

Classic sections, such as those recorded by Mantell (1822) in the Lewes district, have long been overgrown and lost, but there are still some exposures in large working quarries southeast of Lewes which present good sections through most of the Cenomanian. Some of these sections were cited by Kennedy (1969), whose work has been closely followed here, and many of the brachiopods he collected are used in the present study. Among the many exposures described by Kennedy are the pits for the cement industry in the Southerham and Glynde areas. Eastwood's Cement Co. pit, Southerham Grey Pit, Newington's pit, Rodmill Cement Works pit near Asham and the Balcombe pit are among those which have yielded many fine brachiopods. As a result of his work on the coastal sections at Folkestone and Eastbourne, Kennedy was able to apply ammonite Zones to sections in the pits (Table 1).

The coastal sections, however, are complicated by numerous faults and superficial slumping, and there is no clear section from Eastbourne towards Beachy Head. South of Cow Gap, the 2–3 m thick Glauconitic Marl can be traced in bluffs at the base of the cliffs to Head Ledge, where it is well exposed and contains brachiopods with well-preserved shells, including the *Grasirhynchia grasiana* (d'Orbigny), *Monticlarella rectifrons* (Pictet) and *Kingena concinna* Owen assemblage.

Approximately 12 m above the basement bed at Eastbourne, a bed containing *Orbirhynchia mantelliana* (J. de C. Sowerby) in abundance forms a recognizable band. It can be better seen where the beds are at beach level on a platform east of Beachy Head. This is band 6 of Kennedy (1969), which occurs at the top of the *Turrilites costatus* Subzone, *Acanthoceras rhotomagense* Zone.

Higher up, at the top of band 9 of Kennedy (*Acanthoceras jukesbrownei* Zone) *Concinnithyris subundata* (J. de C. Sowerby) occurs with a marked variant *burhamensis* Sahni, but specimens of

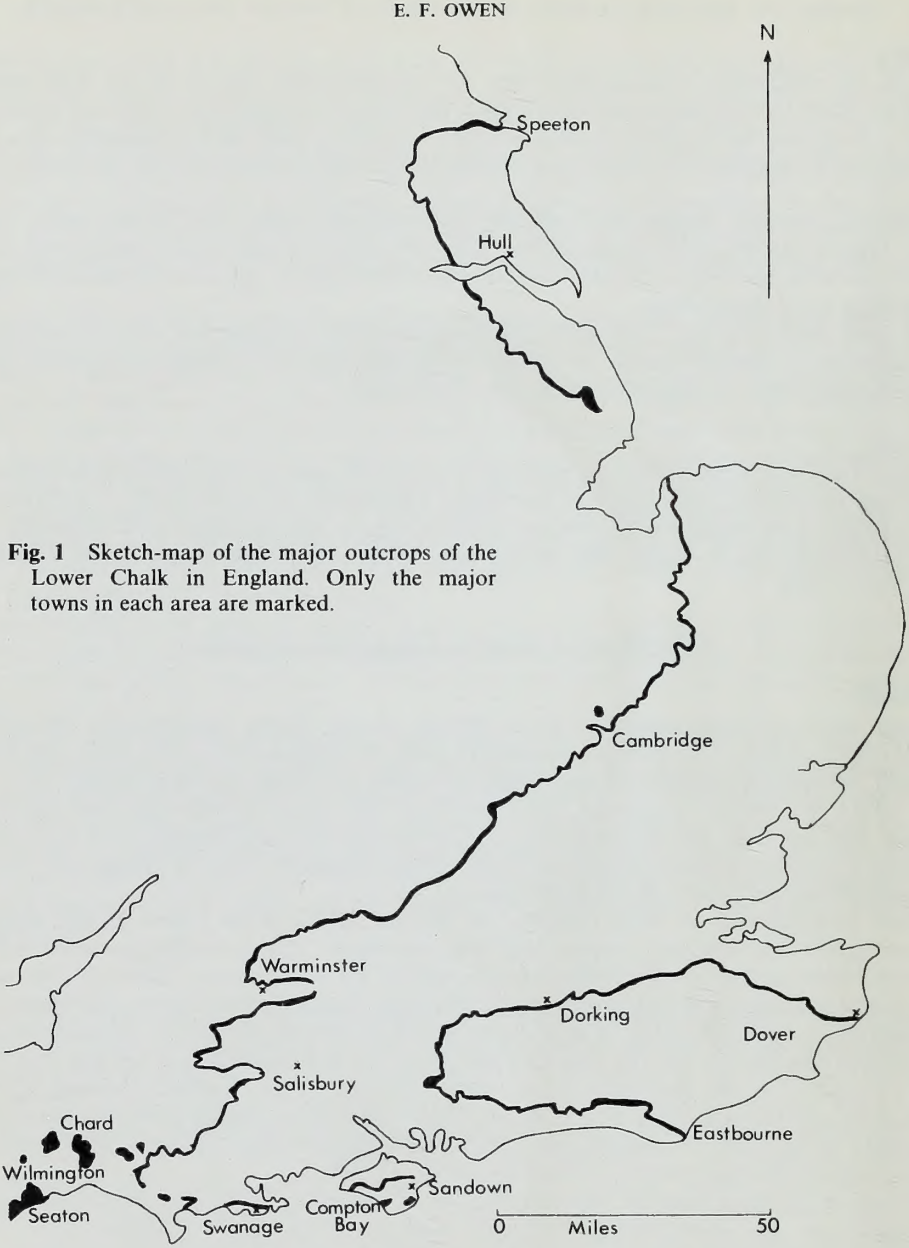


Fig. 1 Sketch-map of the major outcrops of the Lower Chalk in England. Only the major towns in each area are marked.

this variety collected here are proportionately smaller than similarly-named forms from the type locality at Burham, Kent.

During the course of a more detailed study of coastal and inland areas of Sussex for a Ph.D. thesis (not completed), Helen Anderson measured sections previously studied by Kennedy. In some cases she reached significantly different results, and she identified two distinct *Orbirhynchia mantelliana* bands: see p. 93. This confirms the unpublished results obtained by C. J. Wood, British Geological Survey (personal communication), from the Channel Tunnel no. 1 (Aycliffe) and Channel Tunnel no. 2 (Dover Pier) boreholes near Dover, and the Fetcham Mill borehole, Leatherhead, Surrey.

Table 1 Zonal schemes for the Cenomanian of Britain and northern Europe.

		North Germany (Wiedmann 1979)	**North Germany** (Ernst & Schmidt 1979)	**Britain** (Wright & Kennedy 1984)		**Boulonnais** (Amedro *et al.* 1976)	**S. E. France** (Thomel 1965)
				zones	subzones		
TURON.	LOWER			*Watinoceras coloradoense*		*Watinoceras coloradoense*	
				Neocardioceras juddi			*Fagesia superstes*
CENOMANIAN	UPPER	*Metoicoceras geslinianum* *Metoicoceras muelleri*	*plenus* Zone	*Metoicoceras geslinianum*		*Metoicoceras* gr. *geslinianum*	*Calycoceras naviculare*
		Lotzeites lotzei		*Calycoceras guerangeri*		*Calycoceras naviculare*	*Calycoceras crassum* *Calycoceras robustum*
	MIDDLE	*Eucalycoceras spathi*		*Acanthoceras jukesbrownei*		*Acanthoceras jukesbrownei*	*Acanthoceras rhotomagense*
			rhotomagense Zone				
		Euomphaloceras cunningtoni		*Acanthoceras rhotomagense*	*Turrilites acutus* *Turrilites costatus*	*Acanthoceras rhotomagense*	*Acanthoceras praecursor*
	LOWER	*Mantelliceras mantelli*	*Mantelliceras mantelli*	*Mantelliceras dixoni*		*Mantelliceras* gr. *dixoni*	*Mantelliceras mantelli*
		Utaturiceras vicinale	*Neohibolites ultimus*	*Mantelliceras mantelli*	*Mantelliceras saxbii* *Neostlingoceras carcitanense*	*Mantelliceras cantianum*	*Mantelliceras saxbii*

Inland exposures along the North Downs

The general succession remains much the same as that seen in the coastal section at Folkestone, although exposures of Glauconitic Marl are not so readily available in this area. The Chalk Marl is well represented with the transition to the more massive Grey Chalk rather better defined than on the coast. The best localities are in the Medway Valley where a series of quarries were described by Dibley (1918) and Kennedy (1969). The brachiopod faunas are in a confused state of nomenclature and are in need of revision. The present work, in addition to being a re-appraisal of Kennedy's work, is aimed at updating and redescribing some of the brachiopod species thought to be of stratigraphical importance. These are, in the main, listed by Kennedy (1969: 482, 485, 486) in his description of the beds exposed at Bluebell Hill, Burham, Kent.

Hampshire

Better known for its Upper Chalk and Tertiary deposits, Hampshire also includes geologically the Isle of Wight, where the Upper Greensand and Lower Chalk are well exposed in the cliff

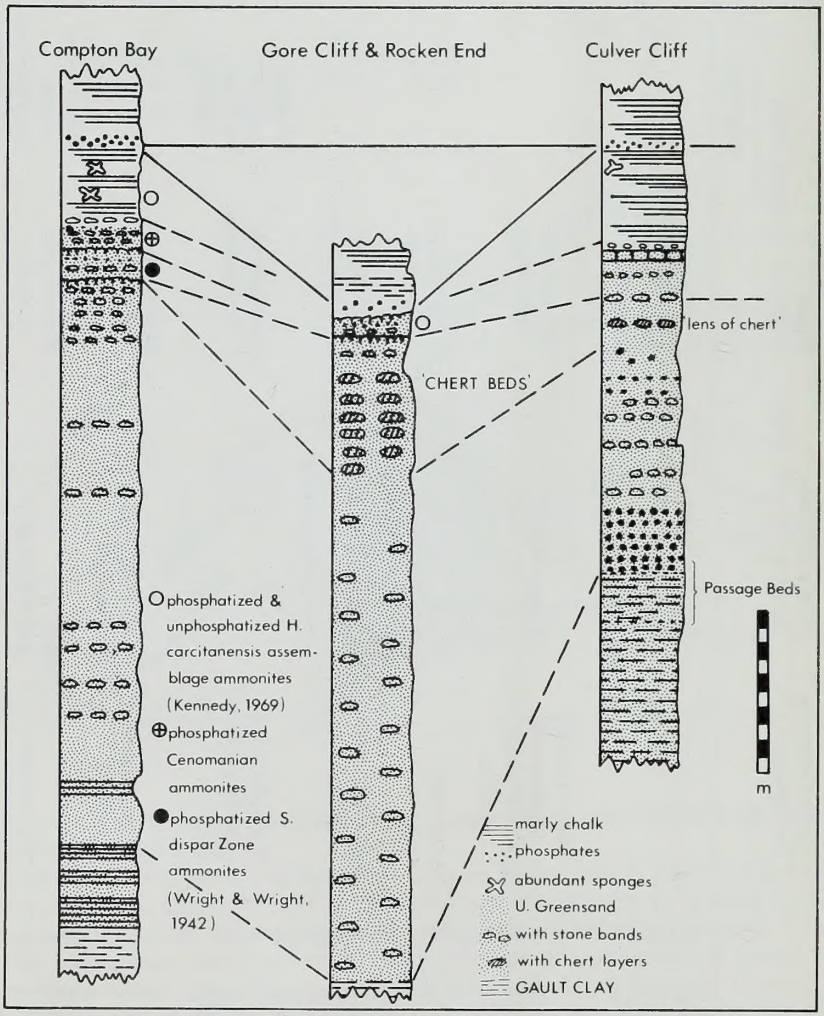


Fig. 2 Correlation of the Upper Greensand and Cenomanian beds exposed at Compton Bay, Gore Cliff and Culver Cliff, Isle of Wight.

sections from Compton Bay in the west to Culver cliff in the east, Fig. 2. The brachiopod fauna is again represented in bands in two distinct facies, the marl beds of the Middle Cenomanian, containing the same or a similar assemblage of *Grasirhynchia grasiana*, *G. martini*, *Kingena concinna*, *Terebratulina protostriatula* sp. nov. (p. 150), and *Orbirhynchia mantelliana*, as on the mainland. The more sandy facies of the Upper Greensand and Glauconitic Marl have a brachiopod fauna similar to those at Eastbourne and the south-western localities in the Warminster and south Devon areas. As in the case of the inland exposures of the Weald, some elements of the fauna appear to be relatively independent of facies and also occur in beds of a more sandy and glauconitic nature, notably *Grasirhynchia grasiana* and *Terebratulina protostriatula* sp. nov. The genus *Cyclothyris*, however, appears to be confined to the coarser sediments, except for *Cyclothyris* sp. and *C. difformis* which have been recorded from the chalky basement beds of Dorset and Wiltshire (Kennedy 1970).

South-western outcrops

Accounts of the Upper Cretaceous of south-west England can be found in the works of Jukes-Browne & Hill (1903–4), Wilson *et al.* (1958), Drummond (1970), Kennedy (1970) and Jarvis & Woodroof (1984).

Dorset. Except at the coast, the brachiopod faunas in Dorset occur mainly in the Chalk Basement Bed. Brachiopods are predominantly Terebratulidae and have been collected from Evershot, Eggardon, Chilfrome, Maiden Newton, Beaminster, Askerswell, Toller Fraterum and Toller Porcorum and other places listed by Kennedy (1970).

Kennedy's (1970) detailed account of the Cenomanian Basement Beds in Wiltshire and north Dorset was accompanied by numerous graphic sections of the sequence indicating the ammonite assemblages and brachiopod faunal bands. This has proved invaluable since, hitherto, only the broadest outlines of horizons and zones were to be found on labels in museums and private collections.

At the coast, especially in the Punfield, Swanage, area, Fig. 3, there is lateral variation in beds of Upper Albian to Cenomanian age. In the cliff section west of Ballard Point, the basal 15 cm of the Chalk Marl contains an *Orbirhynchia mantelliana* band with associated *Grasirhynchia*

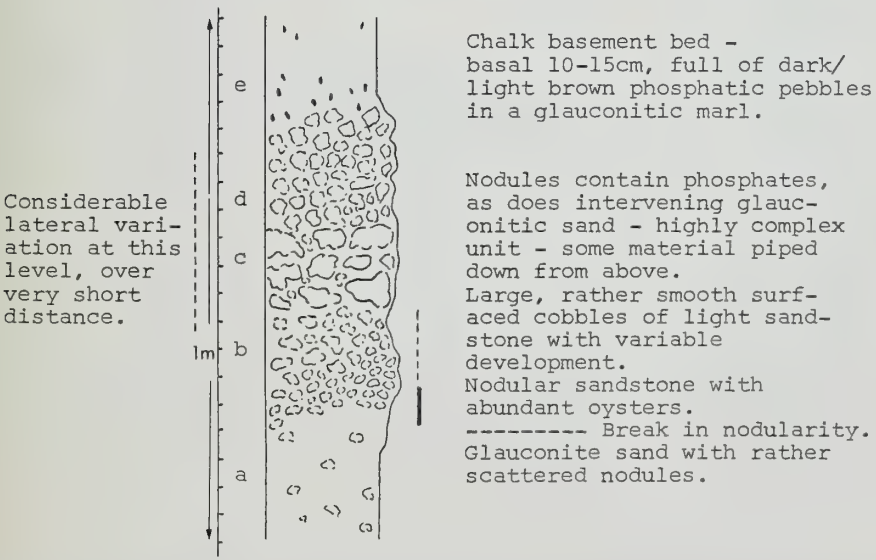

Considerable lateral variation at this level, over very short distance.
1m
e
d
c
b
a
Chalk basement bed - basal 10-15cm, full of dark/ light brown phosphatic pebbles in a glauconitic marl.
Nodules contain phosphates, as does intervening glauconitic sand - highly complex unit - some material piped down from above.
Large, rather smooth surfaced cobbles of light sandstone with variable development.
Nodular sandstone with abundant oysters.
--------- Break in nodularity.
Glauconite sand with rather scattered nodules.

Fig. 3 Vertical section through part of the Upper Albian and Cenomanian at Ballard Point near Punfield Cove, Swanage Bay, Dorset. The *Dereta pectita ballardensis* beds occur at the base of the nodular sandstone with oysters.

grasiana and an undescribed *Concinnithyris* sp. The Cenomanian Basement Bed (Fig. 3e) is of Middle Cenomanian age, and rests on a highly complex unit (Fig. 3b–d) containing phosphatic nodules and glauconitic sands showing evidence of piped material from the beds above. It contains both Upper Albian and Cenomanian ammonites. A layer of limestone boulders forms a convenient marker separating the Cenomanian beds from the underlying Albian beds (Fig. 3a) with numerous *Amphidonte obliquata* (Pulteney). Just beneath these boulders is a bed containing examples of *Dereta pectita* that differ from the typical form described by J. Sowerby (1816) from Horningsham, Wiltshire, in their subquadrate outline, larger foramen and coarser ornament of radiating costae. This distinctive form is described here as *Dereta pectita ballardensis* subsp. nov. (p. 162).

Devon. The farthest western outcrop of Cenomanian rocks occurs in the Haldon Hills (Hamblin & Wood 1976; Wood *in* Selwood *et al.* 1984), but the succession can be more readily studied at the coast between Branscombe and Humble Point where this part of it is well

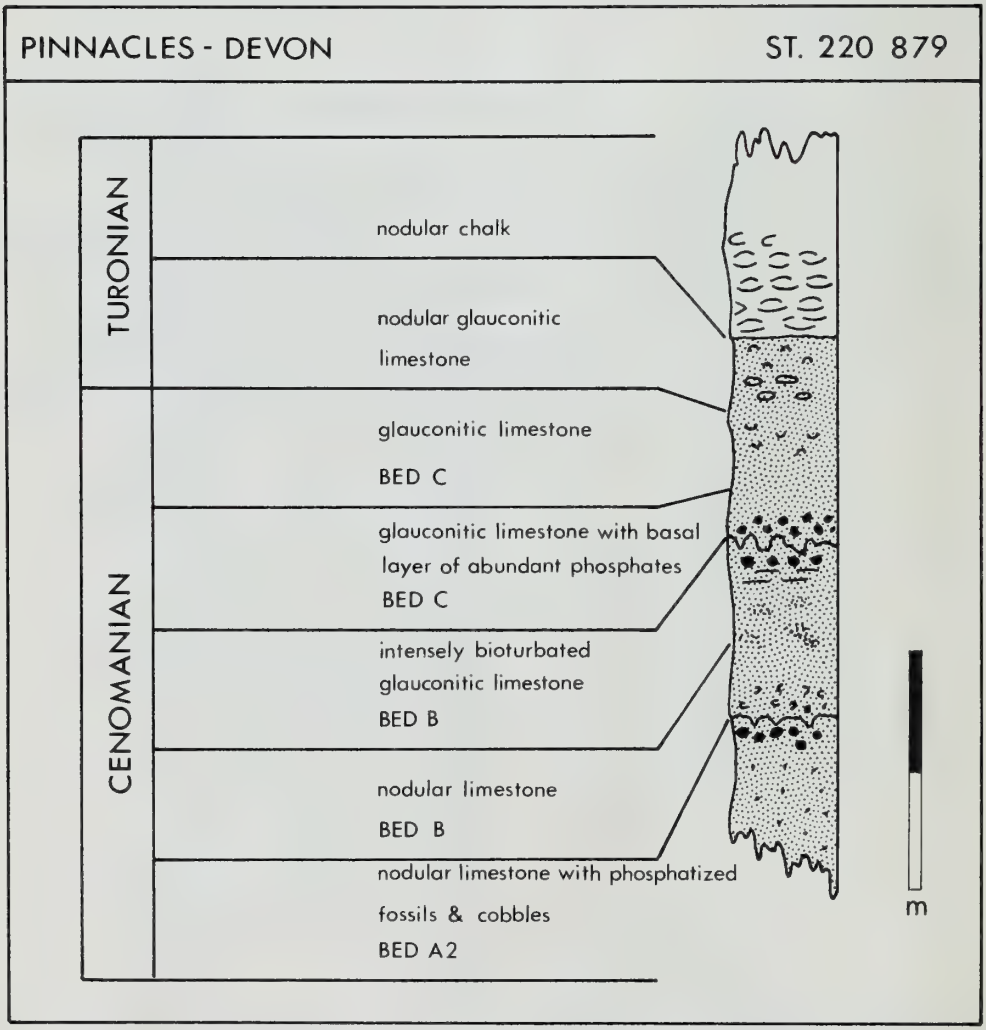


Fig. 4 Vertical section through the Pinnacles, Devon, showing the expanded Beds C and B which are well exposed.

exposed, although totally different in development. Here the four lithological units described by Jukes-Browne (1903) as divisions A, A2, B and C, can be examined. They were revised by Jarvis & Woodroof (1984), who gave new names to the divisions. The oldest, division A (Pounds Pool and Hooken of Jarvis & Woodroof), is a coarse shaly limestone with glauconite and fragments of quartz, and is very fossiliferous. Although some of the ammonites in these beds show signs of reworking, the molluscan and brachiopod faunas are well preserved, with specimens of *Cyclothyris difformis* (Valenciennes *in* Lamarck), *Dereta pectita* (J. Sowerby) and *Kingena arenosa*

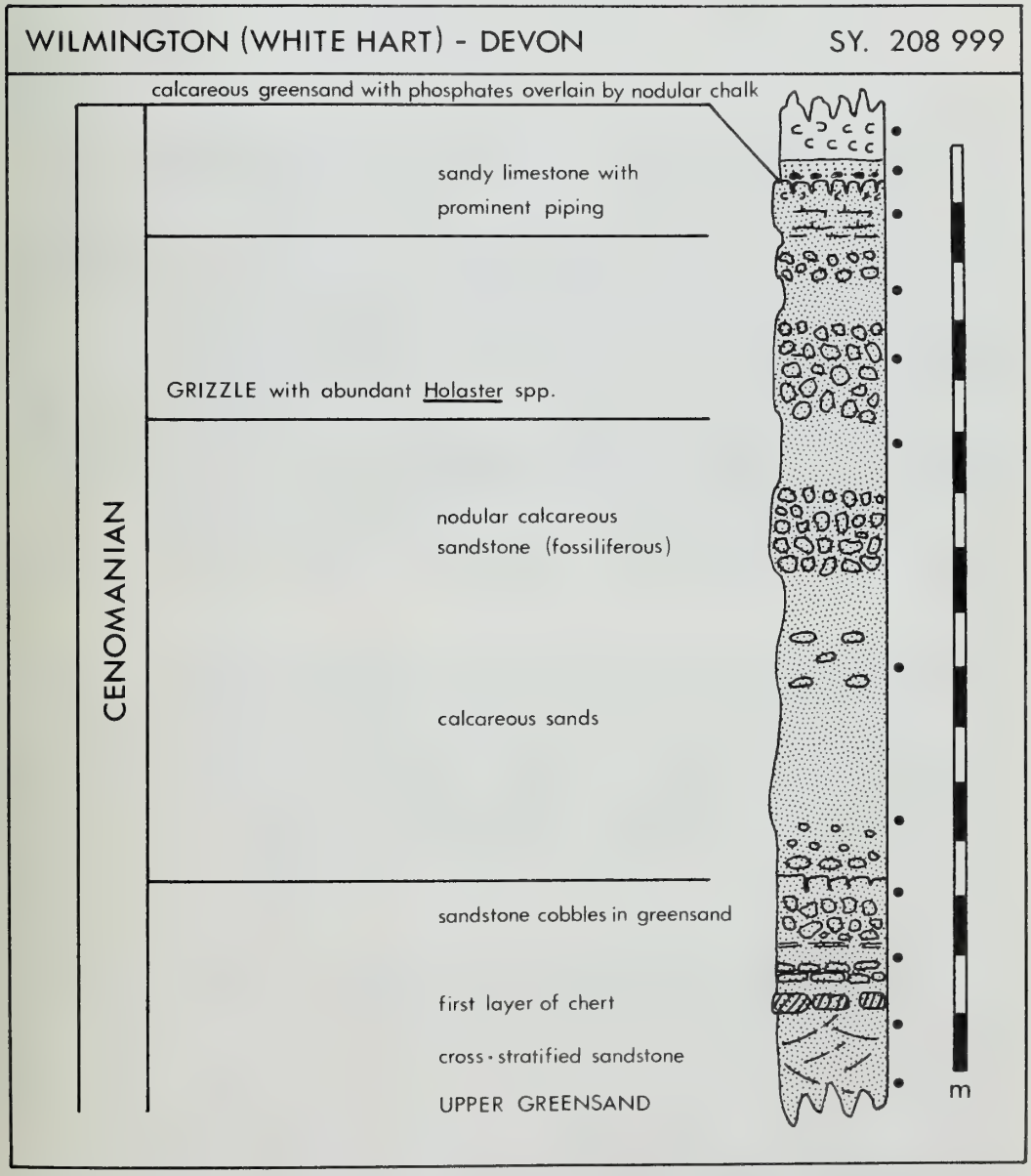


Fig. 5 Section at White Hart sand pit, Wilmington, Devon, showing the extent of the calcareous sands and the Grizzle above. See also Smith *et al.* (1988: 8).

(d'Archiac). According to Kennedy (1970) the age is *Mantelliceras saxbii* Subzone, *M. mantelli* Zone.

Bed B (Little Beach of Jarvis & Woodroof) is a finer, highly glauconitic, white sandy limestone containing no brachiopods but having ammonites of the *Mantelliceras dixoni* Zone.

Bed C (Pinnacles of Jarvis & Woodroof) is developed on the coast as a hard, gritty, highly glauconitic nodular chalk, streaked with red and green veins and highly burrowed with *Thalassinoides paradoxica*. There are three ammonite assemblages: phosphatized *jukesbrownei* and *guerangeri* Zone elements, glauconitized *geslinianum* elements and indigenous ? *geslinianum* Zone elements, and numerous bivalves, serpulids and bryozoans. The brachiopod fauna consists of *Orbirhynchia wiesti* (Quenstedt), *O. multicostata* Pettitt, *Concinnithyris* sp. and *Arcuatothyris rugulosa* (Morris). This is a similar brachiopod fauna to that of the Plenus Marl elsewhere.

W. E. Smith (1957*a*, *b*, 1961) described the lateral variations in the lithology and thickness of the coastal outcrops and some of their inland equivalents, particularly those exposed in the two sandpits in the Wilmington district further north. These pits, Hutchin's sandpit (ST 216003) and the more accessible White Hart sand pit (SY 208999), Fig. 5, were reviewed by Kennedy (1970: 66, 665). Carter & Hart (1977: 99, 100) reviewed the work on the basis of planktonic microfaunal evidence, but their findings do not alter the information regarding the position of the brachiopod-bearing beds. Jarvis & Woodroof (1984) have now given what might be a more acceptable explanation of the age and position of the beds in this section. The lithostratigraphy of the Wilmington section and its correlation with the coastal section have recently been fully documented by A. B. Smith *et al.* (1988).

The Wilmington outlier consists of loose-bedded sands, sandy nodular limestones and glauconitic chalk. The nodular limestone or 'Grizzle' contains a rich fauna of molluscs, echinoderms and brachiopods. *Mantelliceras* spp., *Schloenbachia* spp., and *Inoceramus virgatus* are commonly associated with a fauna of predominantly rhynchonellid brachiopods. *Cyclothyris difformis* is a particularly common species, occurring with *Dereta pectita*, *Terebrirostra lyra*, *Arenaciarcula beaumonti*, *Monticlarella brevirostris*, *Orbirhynchia wilmingtonensis* sp. nov., *Ovatathyris ovata* and *Kingena arenosa*. An example of the north German species *Gemmarcula canaliculata*, which also occurs at Wilmington and Tournai, Belgium, is figured here, Pl. 17, figs 19–21.

Eastern outcrops

The Cambridge Greensand was formerly exposed in phosphate workings south and east of the town. Nowadays, sections are confined to those incidental to chalk workings, as in the Rugby Cement Co. quarry at Barrington, where it is possible to see the Cambridge Greensand with the overlying Chalk Marl and Totternhoe Stone. The age of the Cambridge Greensand has been much discussed: Carter & Hart (1977), from microfaunal evidence, believe that it belongs to the *Neostlingoceras carcitanense* Subzone, at the base of the Lower Cenomanian. Brachiopods occur chiefly at the base of the Cambridge Greensand. Many are crushed, decorticated and phosphatized, and are believed to have been derived from the Upper Albian (Morter & Wood 1983). In the Fulbourne area, where the Lower Chalk is well exposed, specimens of *Ornatothyris sulcifera* (Morris) have been found in the top 2–3 m of the section. The full geological range of this species, however, is not known.

The Plenus Marls are represented in the Cambridge area, but are reduced in thickness. The characteristic rhynchonellid *Orbirhynchia multicostata* is present in moderate numbers but the zone fossil, the belemnite *Actinocamax plenus*, is rare in this district.

Norfolk

The Cretaceous rocks exposed on the Norfolk coast include the Red Rock of Hunstanton Cliff which rests on the Carstone and represents the Middle to Upper Albian in East Anglia. It consists of three distinctly different lithologies which have been distinguished by various authors as Beds A, B & C or their equivalent beds 3, 2 & 1 (Fig. 6). More recently, Gallois & Morter (1978) have introduced another numerical scheme for these beds which begins at the

Fig. 6 The cliff section at Hunstanton, Norfolk, to show Beds A, B, and C of the Red Rock, the *Inoceramus* Bed and the Totternhoe Stone.

dentatus Zone of the Middle Albian and ends at Bed 19 at the top of the *dispar* Zone of the Upper Albian. Brachiopods occur in Beds 13 to 16 where the fauna is dominated by *Moutonithyris dutempleana*, *Orbirhynchia parkinsoni* and *Kingena spinulosa*, species which are indigenous in the basal beds of the Cambridge Greensand, considered to be of Lower Cenomanian age. These beds are condensed and only a few metres thick at Hunstanton, and correlation with the much thicker succession in Lincolnshire and Yorkshire is difficult (Morter & Wood 1983).

The hard bands of consolidated limestone known as the 'Paradoxica' Bed, chalkstone with a hardground, and the *Inoceramus* Beds, marls rich in bioclastic debris, are clearly visible above the Red Rock at Hunstanton (Fig. 6). They contain a varied brachiopod fauna of *Ornatothyris* spp., *O. pentagonalis*, *Concinnithyris* sp. and *Kingena concinna*.

North-east England

The paucity of ammonites in the Cenomanian of Lincolnshire, Humberside and North Yorkshire has made direct correlation with beds of equivalent age in southern England very difficult. Certain well-marked lithological horizons have been recognized, however, and can be equated with beds in eastern and southern England. Brachiopod faunas in these lithological bands have become more important since Bower & Farmery (1910), Jefferies (1963) and Jeans (1973) indicated brachiopod bands which appear to be common to both northern and southern areas.

Bower & Farmery (1910) established a numerical system for the beds in the Lower Chalk of Lincolnshire which was broadly applicable to the entire northern province. Their Bed I comprised the 'Paradoxica' Bed and the two *Inoceramus* Beds. Between these and the Grey Bed (Totternhoe Stone), a series of hard bluish-grey chalk beds occur, within which a band of

Orbirhynchia sp. is well developed; Jeans (1968) called it the Lower *Orbirhynchia* Bed. Bower & Farmery attached a great deal of importance to the existence of two bands in their Beds V–IX, the Lower and Upper Pink Bands occurring above the Totternhoe Stone. The Lower Pink Band is the more fossiliferous and contains *Grasirhynchia martini*, *Kingena concinna* and *Terebratulina ornata* (Roemer) (described here as *Terebratulina imbricata* sp. nov., p. 148). The presence of large numbers of *T. ornata* suggested to these authors that the Lower Pink Band could be called the *T. ornata* Subzone. Wright & Wright (1942) recorded many *Terebratulina* from the Lower Pink Band in Yorkshire.

A burrowed erosion surface at the top of Bed IX is overlain by Bed X, a conglomerate at the base followed by the laminated marls of the Black Band, both of *Neocardioceras juddi* Zone, Upper Cenomanian, age. The conglomerate is highly fossiliferous and contains *Monticlarella jefferiesi*, *Orbirhynchia multicostata* and *Ornatothyris* sp., a brachiopod assemblage referred to by Jefferies (1963) who concluded that it characterized the upper part of the Plenus Marls.

Northern Ireland

Upper Cretaceous sediments outcrop around the margins of the Antrim basalt plateau, but Cenomanian deposits are restricted to the south-east in Co. Antrim. Here they consist of a series of sands forming part of the Hibernian Greensands extending from south of Belfast to Portmuck, north of Island Magee. The stratigraphy has been revised by McGugan (1957), Reid

Fig. 7 Sketch-map showing the major outcrops of Cenomanian rocks in the Belfast area and Co. Antrim.

(1958a, b, 1971), Hancock (1961), Fletcher (1977) and Fletcher & Wood (1983). The sediments consist of two main stratigraphical units, the Hibernian Greensand (Cenomanian to Middle Santonian) and the Ulster White Limestone (Santonian to Maastrichtian). The Hibernian Greensand includes the Belfast Marls (a new name by Fletcher & Wood, 1982, for the Glauconite Sands) which are of *Mantelliceras mantelli* Zone age. This unit yields brachiopods in the Island Magee area, including *Cyclothyris* sp., *Orbirhynchia* sp., *Capillithyris squamosa* and indeterminate Terebratulidae. The brachiopod fauna has never been adequately investigated and is in need of revision.

The succeeding Island Magee Siltstone Member (Fletcher & Wood 1982) consists of grey argillaceous sandstones with hard calcareous bands, and is of upper *Acanthoceras rhotomagense* Zone age. It is followed non-sequentially by the Colinwell Sands, in which brachiopods are fairly common, but are not identifiable, and are again in need of revision.

Northern France

At Cap Blanc Nez in the Boulonnais the succession is much the same as at Dover and Folkestone, and the Lower Chalk, although somewhat more compact, contains an identical brachiopod fauna. Amedro *et al.* (1976, 1978) divided this part of the succession into ten parts, with a letter and a numeral, C–L and 1–27, to denote its position in the top of the Albian and

Fig. 8 The distribution of the major outcrops of Lower Chalk in NW France.

the Cenomanian. Numerous specimens of *Orbirhynchia mantelliana* occur in Bed H towards the top of Band 19. This is near the top of the *T. costatus* Subzone and corresponds exactly to the two *O. mantelliana* Bands of southern England discussed earlier. I have collected specimens of *O. mantelliana* from a similar band at Cran d'Escalles and, from a bed just below, examples of *Kingena concinna*, *Modestella geinitzi*, *Grasirhynchia grasiana*, *G. martini* and *Capillithyris squamosa* (E. F. & M. M. Owen collection, British Museum (Natural History)).

The classic coastal section at St Jouin, reviewed by Juignet & Kennedy (1976) is typical of the coastal exposures in Normandy. Lithological variations include cherty bands with sponge spicules, hard limestones, and bands of marl and sandy limestones. *Kingena arenosa*, though somewhat smaller than the typical form from the Tourtia of Belgium, occurs in the Lower and Middle Cenomanian limestones associated with *Terebrirostra lyra* and *Dereta pectita* which are also smaller than in England. At Octeville and Cap de la Hève, where the glauconite is more concentrated, there is a predominance of Rhynchonellidae. Here, as in Dorset and Devon, *Cyclothyris difformis* is a comparatively common fossil occurring with other brachiopods in the coarser sandy facies.

The Cretaceous beds in the Rouen area are affected by the Vernon–Rouen–Pavilly anticlinal axis, and the basal Cenomanian is seen only at Rouen where it consists of bioturbated glauconitic sands resting on grey clays of the Upper Albian. Above this basement bed are 20 m of the Craie Glauconieuse with bands of black chert and hardgrounds, of *Mantelliceras mantelli* Zone age, and containing specimens of *Cyclothyris* cf. *difformis* and *Grasirhynchia grasiana*. Above the Craie Glauconieuse are 2 m of Craie de Rouen, of *Acanthoceras rhotomagense* Zone age, and in the chalk above the large terebratulid *Concinnithyris obesa* (J. de C. Sowerby) occurs in association with *Arcuatothyris rugulosa*, *Capillithyris squamosa disparilis* (d'Orbigny) and *Orbirhynchia* cf. *paucicostata* (Roemer).

The chalky facies of Rouen can be traced eastwards through Orne, where it interdigitates with the sandy facies at Le Mans (Sarthe). Here the fauna changes once more; *Cyclothyris compressa* (Valenciennes *in* Lamarck) characterizes the Upper Cenomanian Sables du Perche, where it occurs with *Gemmarcula menardi* (Lamarck), an example of which is figured here (Pl. 17, figs 4–6), *Sellithyris tornacensis* (d'Archiac) and *S. phaseolina* (Lamarck). Similar assemblages occur at Briollay, Mayet and Mezières-sous-Ballon.

At Bousse, the fine-grained chalk of the Sables de Bousse contains *Sellithyris phaseolina* (Lamarck) and *Orbirhynchia boussensis* sp. nov. (p. 103). In the Charente, where the sediments are fine compact chalk, *Sellithyris phaseolina* occurs, in association with *Gemmarcula carantonensis* (Pl. 17, figs 22–24).

East of the Paris Basin, a few exposures of Cenomanian age yield brachiopods. At Vitry (Marne) *Concinnithyris obesa* occurs rarely in the chalky facies, and at Brienne-le-Château (Aube) an *Orbirhynchia* sp. similar to *O. mantelliana* (J. de C. Sowerby) has been found.

Belgium

The brachiopods in the Cenomanian Tourtia deposits at Tournai and Gussignies are similar in some respects to the faunas from Wilmington, Devon, the Essen Greensand and the Münster Basin. However, Rhynchonellidae are predominant at Wilmington, while Terebratulidae and Terebratellidae are predominent at the Belgian localities and at Essen.

Most of the Cenomanian Tourtia occurs around Tournai and Mons and has a very distinctive and varied brachiopod fauna. The Rhynchonellidae include *Cyclothyris scaldisensis* (d'Archiac) and *Orbirhynchia* cf. *paucicostata* (Roemer), while the Terebratulidae are dominated by *Rectithyris depressa* (Valenciennes *in* Lamarck), *Capillithyris capillata* (d'Archiac) and *Sellithyris tornacensis* (d'Archiac). The Terebratellidae include *Arenaciarcula beaumonti* (d'Archiac) and *Gemmarcula canaliculata* (Roemer) (see Pl. 17, figs 22–24), which also occur at the north German localities, while *A. beaumonti* occurs also in Poland and at Wilmington, Devon.

Germany

In the Münster Basin, the Cenomanian occurs as many different facies which include arenaceous, calcareous and glauconitic marl developments. The more fossiliferous outcrops are

Fig. 9 The major Cenomanian outcrops of north Germany, and the Dresden and Regensburg districts.

mainly in the southern part of the basin in the Essen Greensand where the fauna is similar to that in the Belgian Tourtia. Additional species not known from the Belgian Tourtia are *Burirhynchia sigma* (Schloenbach), *Arcuatothyris arcuata* (Roemer) and a large undescribed terebratulid, similar to *Concinnithyris davidsoni* from the Upper Greensand of Warminster.

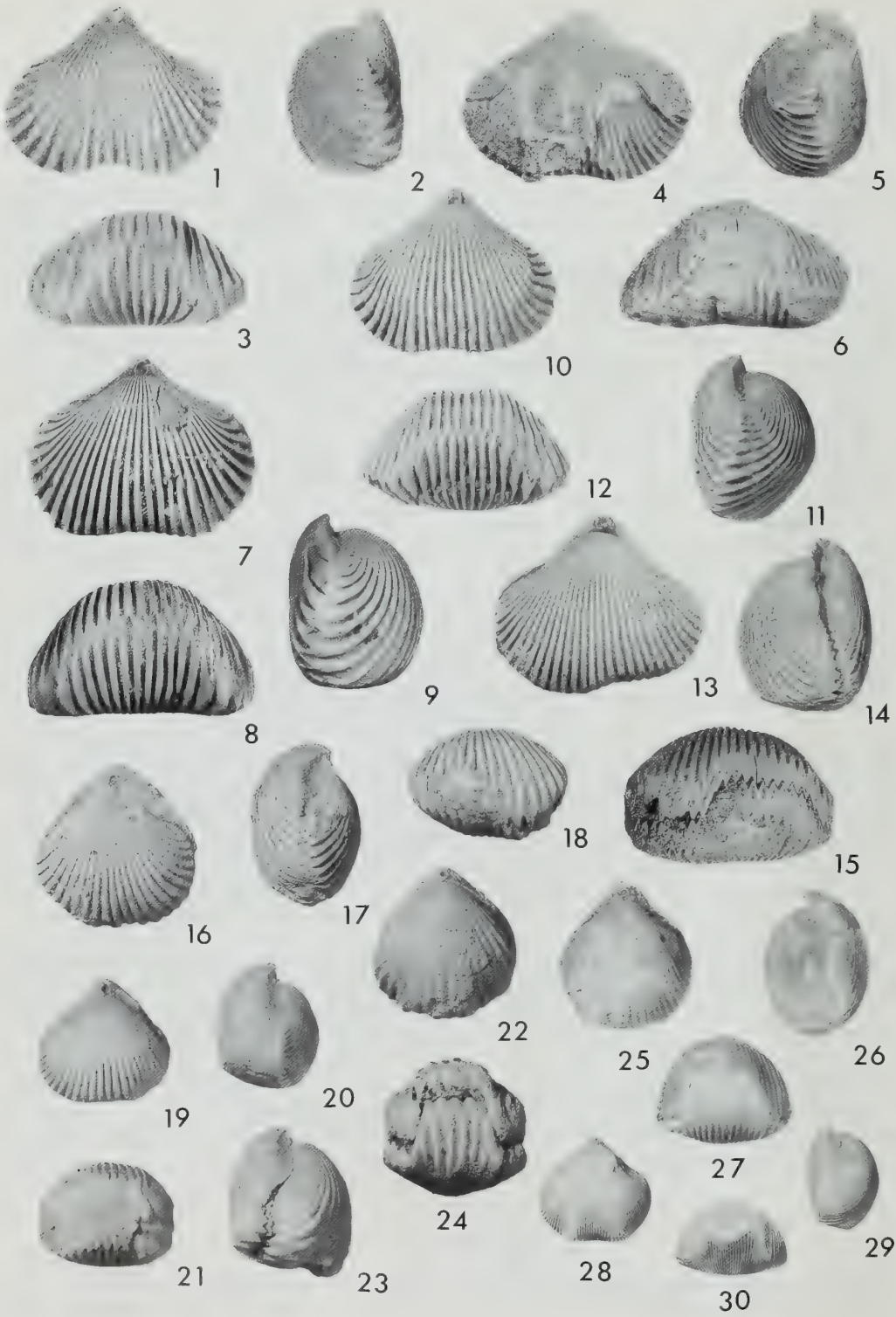
Further east at Flöteberg (Tecklenberg), Langelsheim and Wunstorf in the Middle Cenomanian marl facies, the familiar *Grasirhynchia grasiana*, *Concinnithyris* cf. *subundata*, *Kingena concinna* assemblage occurs, although the lithology is a harder, more compact marly limestone than occurs in France or southern England.

A fauna similar to that of the Grès du Mans in the Sarthe occurs in the Bryozoensandstein at Morasheimer. Lehner (1937) listed *Gemmarcula menardi*, *Sellithyris phaseolina* and *Cyclothyris compressa*. The Upper Cenomanian is also represented at the Kassenberg, Mülheim, where a species of *Orbirhynchia* occurs that is similar to *O. boussensis* sp. nov. of the Sables de Bousse, Sarthe.

In the basal conglomerate of the *Actinocamax plenus* Zone at Ratsteinbruch, Dresden, large *Cyclothyris sudetica* (Geinitz) occur in pockets of softer rock. The same species also occurs in the Lower Sandstone at Regensberg, Bavaria. Associated faunas include undescribed Terebratulidae, probably of the genus *Sellithyris*.

Systematic descriptions

The present research was never intended to be taken as a comprehensive monograph of all known species of brachiopods in the Lower Chalk, since many of these have been adequately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described or revised in recent years and are in little need of additional remarks. Problematic subjects have been investigated and the results and their interpretations fully explained. The extensive use of transverse serial sections, revealing the internal structures of Chalk Terebratulidae, has somewhat altered the established or more conventional interpretation, based largely on dissected specimens, of M. R. Sahni (1929).

Full synonymies are of limited value where in the cited works there is no reliable horizon correlation and no convincing illustration accompanying a description of a species and, therefore, such items are excluded from the synonymies in the present work.

This section deals with existing genera and species (some with new descriptions) and describes new taxa where these are considered to be stratigraphically important. Unless otherwise stated, the material described or referred to is in the collections of the Department of Palaeontology, British Museum (Natural History), where specimen numbers are normally prefixed B or BB, but reference to material from other collections is denoted by the following prefixes:

SM = Sedgwick Museum, Cambridge
BGS = British Geological Survey (formerly Institute of Geological Sciences)
GM = Museum d'Histoire Naturelle, Geneva.

In the figures of serial sections the numbers shown by each section give the distance in mm from the umbo to the first section, thereafter the distance between sections. In the plate descriptions, SEM = scanning electron micrograph.

The following terms are used: **Outline**—the complete shell outline viewed dorsally or ventrally. **Profile**—the complete shell outline viewed from either side, or from the front. **View(ed)**—the surfaces seen in the described aspect, e.g. 'anterior view' includes details of the commissure. In describing ribbing the terms 'costa', 'costella' etc. are used in the sense of prominence or frequency of ribs, not in relation to their origins.

Class **INARTICULATA** Huxley, 1869

Superfamily **LINGULACEA** Menke, 1828

Family **LINGULIDAE** Menke, 1828

Genus ***LINGULA*** Bruguière, 1797

Lingula subovalis Davidson

Pl. 5, fig. 32

1852 *Lingula subovalis* Davidson: 7; pl. 1, figs 29, 30.

LECTOTYPE. B8291, here selected from three syntypes in the Davidson Collection. Dimensions: length 12·6 mm, width 7·5 mm.

PLATE 1

Figs 1–9 *Cyclothyris punfieldensis* sp. nov. Figs 1–3, Glauconitic Marl, Undercliff, Isle of Wight. Paratype BB82244, × 1½. Figs. 4–6, Upper Albian, Dispar Zone, Punfield Cove, Dorset. **Holotype** BB82245, × 1½. Figs 7–9, Basal Cenomanian, Cap de la Hève, Normandy. BB82183, × 1½.

Figs 10–12 *Cyclothyris* cf. *punfieldensis* sp. nov. Bottom Bed of Upper Albian, Cap de la Hève, Normandy. BB82182, × 1½.

Figs 13–15 *Cyclothyris difformis* (Valenciennes, *in* Lamarck). Upper Greensand, Compton Bay, Isle of Wight. BB82339, × 1½.

Figs 16–18 *Cyclothyris* sp. Albian, Castellas, Narbonne, SW France. BB82367, × 1.

Figs 19–21 ? *Cyclothyris* sp. Lower Cenomanian, Chardstock, Devon. B8218, × 2.

Figs 22–24 *Burrirhynchia devoniana* sp. nov. Lower Cenomanian, White Hart sand pit, Wilmington, Devon. **Holotype** BB82252, × 2.

Figs 25–27 *Burrirhynchia* cf. *sigma* (Schloenbach). Lower Cenomanian, Annopol, Poland. BB82340, × 2.

Figs 28–30 *Burrirhynchia leightonensis* (Walker). Lower Albian, Shenley Hill, Leighton Buzzard, Bedfordshire. B26575, × 1.

EMENDED DESCRIPTION. The outline is regularly elliptical, oval, with subparallel lateral margins; the valve being slightly convex with an umbonal carina not extending more than one third of its length. The surface is smooth, marked only by numerous concentric growth-lines.

REMARKS. Living species of *Lingula* have a habitat restricted to burrows, usually on sandy or silty shorelines, and sometimes near river estuaries. Their tolerance to depth and temperature is limited and, if it can be assumed that their habitats to-day are comparable to those of fossils, lingulas can provide useful evidence of climate and depth.

Apart from the Craniidae, families of inarticulate brachiopods are rare throughout the Mesozoic. Species of *Lingula* have been recorded from the Lower Cretaceous Speeton Clay from time to time and also occur, though somewhat sporadically, within the Lower Greensand in southern England and the Isle of Wight. *Lingula truncata* (J. de C. Sowerby) has been collected from the Upper Aptian of Sandown and specimens from the Hythe Beds of Kent are in the Sedgwick Museum, Cambridge. In France a species described by d'Orbigny (1847) as *L. raulin-iana*, from probable Upper Aptian clays of Grandpré (Meuse), is possibly a synonym of Sowerby's *L. truncata*.

Records from the Albian are sparse but include a specimen identified by Lang (1904) from the 'Gault' of Black Ven, near Lyme Regis, Dorset. Donovan (1949) recorded *Lingula subovalis* from the Albian of Geographical Society Island, Greenland, but this is a misidentification.

There are more records from the Cenomanian, most of which have been identified as *Lingula subovalis* or *Lingula* sp. and include specimens from Butser (Hampshire), Halton, and the Burwell Rock of Burwell (Cambridgeshire). The youngest specimen recorded from the Cenomanian was identified and figured as *Lingula* sp. from the Plenus Subzone, Bed 1, at Merstham, Surrey, by Jefferies (1962).

Class **ARTICULATA** Huxley, 1869

Superfamily **RHYNCHONELLACEA** Schuchert, 1900

Family **RHYNCHONELLIDAE** Gray, 1848

Subfamily **CYCLOTHYRININAE** Makridin, 1955

Genus ***CYCLOTHYRIS*** M'Coy, 1844

Cyclothyris difformis (Valenciennes, *in* Lamarck)
Pl. 1, figs 13–15; Pl. 2, figs 4–6, 10–15

1819 *Terebratula difformis* Valenciennes, in Lamarck: 255; indic. *Encyclopédie Méthodique* (Tabl. Vers, Coquilles, Mollusques et Polypiers **2**): pl. 242, figs 5 (1789). Paris.
1821 *Terebratula dimidiata* J. Sowerby: 138; pl. 277, fig. 5.
1822 *Terebratula gallina* Brongniart: 8; pl. 9, fig. 2.
1828 *Terebratula deformis* Lamarck (*sic*); Defrance: 160; pl. 5, fig. 3.
1849 *Rhynchonella compressa* (Lamarck); d'Orbigny: 35; pl. 497, figs 1–6.
1850 *Terebratula difformis* Lamarck; Davidson: 433; pl. 15, fig. 48.
1852 *Terebratula compressa* Lamarck; Davidson: 80; pl. 11, figs 4 & 5.
1882 *Terebratula difformis* Lamarck; Quenstedt: 696; pl. 54.
1900 *Rhynchonella difformis* (Lamarck); Jukes-Browne: 65, figs 41, 42.
1918 *Terebratula difformis* Valenciennes, *in* Lamarck; Clerc & Favre: pl. 15, fig. 84.
1962 *Cyclothyris difformis* (Valenciennes, *in* Lamarck) Owen: 51; pl. 5, figs 1–7.

LECTOTYPE. Lamarck Collection, Museum d'Histoire Naturelle, Geneva, No. 48; from the Lower Cenomanian, Normandy coast; selected by Owen (1962).

REMARKS. This species was redescribed in a general revision of *Cyclothyris* M'Coy by Owen (1962: 51), where a pictograph illustrated thirteen morphological variants of *C. difformis* (Valenciennes, *in* Lamarck). The present work confirms this variation and adds examples from several different localities. Pl. 2, figs 1–3 represents the acutely triangular form from the Glauconitic Marl of Compton Bay, Isle of Wight and figs 4–6 show an example of a rare form from the Lower Chalk Basement Beds of Snowdon Hill, Chard, Somerset, in which the anterior

commissure is asymmetrical. In some assemblages specimens with either right or left asymmetry are found; for example that figured as Pl. 2, figs 10–12, from the Lower Cenomanian of High Melcombe, Dorset, shows an asymmetrical specimen with left side prominent, and with a greater number of costae and more numerous concentric growth-lines than on the Chard specimen.

Cyclothyris punfieldensis sp. nov.
Pl. 1, figs 1–12; Pl. 2, figs 16–18

Diagnosis. Transversely oval to broadly triangular in outline; adults measure approximately 18·2 mm in length, 14·6 mm wide and 14 mm thick. Umbo slightly produced, beak suberect. Large circular foramen surrounded by extended deltidial plates. Anterior commissure low, arcuate. Dorsal fold poorly developed. Ornament of 30–34 strong, angular, deeply incised radiating costae.

Name. From the type locality of Punfield Cove.

Description. The broadly oval outline, poorly developed concentric growth lines and faintly sulcate median dorsal fold are characteristic of this species. In lateral profile the shell is strongly dorsi-bioconvex, with more inflated dorsal umbonal regions. The consistently arcuate commissure shows no sign of the asymmetry so typical of *Cyclothyris difformis* (Valenciennes, *in* Lamarck) and it can be distinguished from this and other species of *Cyclothyris* in having a faint anterior sulcation in the dorsal fold of adult specimens.

Holotype. C. W. & E. V. Wright Collection, BB82245; from the Upper Albian, Dispar Zone; Punfield Cove, Dorset. Length 18·5 mm; width 14·9 mm; thickness 14·0 mm. Pl. 1, figs 4–6.

Other material. In addition to the holotype the following is a paratype: BB82244; Glauconitic Marl; Undercliff, Isle of Wight. Length 18·2 mm; width 13·3 mm; thickness 12·7 mm. Pl. 1, figs 1–3. Two other specimens are in the BM(NH), BB82183 (Pl. 1, figs 7–9) and BB82184. Other examples are in the British Geological Survey, BGS 110218–110225, Cunnington Collection from the Upper Greensand of Warminster, Wiltshire. A gerontic example BB82341 is shown in Pl. 2, figs 16–18.

Remarks. It is probable that in Britain this species is confined to the topmost Upper Albian, although very similar, conspecific examples occur in the topmost Upper Albian and basal beds of the Cenomanian at Cap de la Hève, Normandy (Pl. 1, figs 7–12). The Normandy examples resemble the British specimens other than in lacking the characteristic slightly produced umbo.

C. punfieldensis resembles *Cyclothyris shenleyensis* (Walker) from the Lower Albian of Leighton Buzzard, Bedfordshire but can be distinguished from that species by its proportionately wider dimensions, deeper brachial sulcation and higher linguiform extension.

Cyclothyris formosa sp. nov.
Pl. 3, figs 1–6

Diagnosis. Triangular in outline, trilobate. Umbo short, massive; beak slightly incurved. Beak-ridges sharp, deltidial plates exposed; interarea fairly extensive. Median dorsal fold well developed. Ventral valve flat to slightly convex, anteriorly sulcate. Anterior commissure with high uniplication.

Name. 'Shapely'.

Description. Convexity of the dorsal valve is regular and its fold, which originated posteriorly at less than one-third of the valve length, becomes increasingly prominent anteriorly to produce a strong anterior trilobation in the shell. The surface ornament, of 34–36 rounded costae, is not interrupted by growth-lines. An average of six to eight costae adorn the median fold with a corresponding number within the pedicle sulcus. Variation within the species is slight, affecting only the degree of uniplication.

HOLOTYPE. BB82206; from the Middle Cenomanian (Lennier's Bed 10), St Juin, Normandy. Length 22·2 mm; width 24·5 mm; thickness 16·7 mm. Pl. 3, figs 1–3.

PARATYPES. BB82207 (Pl. 3, figs 4–6), BB82300–31.

REMARKS. *Cyclothyris formosa* can be distinguished from *C. difformis* (Valenciennes, *in* Lamarck) by its trilobate form, short massive umbo, smaller foramen, lack of asymmetrical development of the anterior commissure and regular biconvexity. It can be distinguished from *C. juigneti* sp. nov. (below), *C. compressa* (Valenciennes, *in* Lamarck) and *Cyclothyris lamarckiana* (d'Orbigny) by general outline, more strongly developed uniplication, more rounded and less deeply incised costae and more regular biconvexity.

Cyclothyris juigneti sp. nov.
Pl. 3, figs 16–21

DIAGNOSIS. Relatively small, triangular in outline. Umbo short, beak suberect, pointed, with large auriculate foramen. Brachial valve convex, median fold poorly developed. Pedicle valve weakly convex. Anterior commissure gently uniplicate with low linguiform extension.

NAME. In honour of Dr P. Juignet, University of Caen, Normandy.

DESCRIPTION. The umbo, though short, has a moderately extensive interarea bounded by sharp beak-ridges. Both valves have approximately 23–25 sharply differentiated costae, with four on the median fold and three in the sulcus. There is no marginal thickening of the valves and growth-lines are not visible.

HOLOTYPE. BB82208; from the Middle Cenomanian, *Turrilites costatus* Zone; La Perrière Orne, France. Length 17·0 mm; width 22·2 mm; thickness 9·8 mm. Pl. 3, figs 16–18.

PARATYPES. BB82209 (Pl. 3, figs 19–21), BB82210–1.

REMARKS. The species can be distinguished from *C. compressa*, *C. difformis* and *C. lamarckiana* by its consistently smaller dimensions, more deeply incised and fewer costae, flatter valves and strongly triangular outline. The dorsal median fold shows about the same degree of development as in *C. compressa* but always remained narrower.

Cyclothyris compressa (Valenciennes, *in* Lamarck)
Pl. 3, figs 22–27

1819 *Terebratula compressa* Valenciennes, *in* Lamarck: 256, no. 54.
1850 *Terebratula compressa* Lamarck; Davidson: 455; pl. 15, fig. 54.
1918 *Terebratula compressa* Valenciennes *in* Lamarck; Clerc & Favre: pl. 19, figs 117, 119.
1962 *Cyclothyris compressa* (Valenciennes *in* Lamarck) Owen: 54; pl. 5, fig. 8.

REMARKS. This species was redescribed by Owen (1962), at which time it was thought to

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PLATE 2

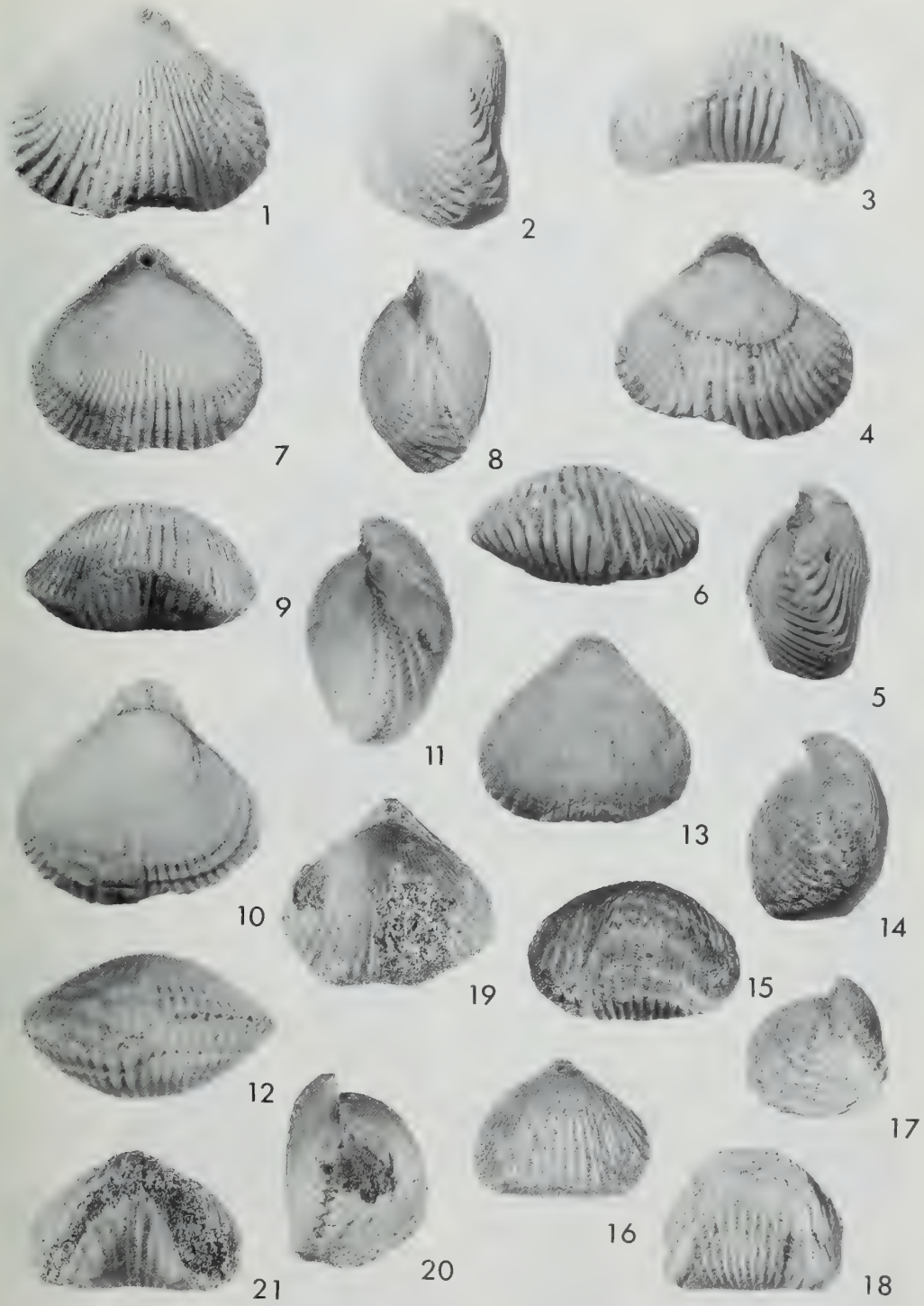
Figs 1–3 *Cyclothyris* cf. *difformis* (Valenciennes, *in* Lamarck). Upper Greensand, Compton Bay, Isle of Wight. BB82248, × 1½.

Figs 4–6, 10–15 *Cyclothyris difformis* (Valenciennes, *in* Lamarck). Figs 4–6, Chalk Basement Bed, Snowdon Hill, Chard, Somerset. BB82242, × 1½. Figs 10–12, Lower Cenomanian, High Melcombe, Dorset. BB82243, × 1½. Figs 13–15, Middle Cenomanian, nodular limestone, Bovey Lane Pit, Devon. BB61120, × 1½.

Figs 7–9 *Cyclothyris scaldisensis* (d'Archiac). Bed B equivalent, Cenomanian, St Jouin, Normandy BB82184, × 1½.

Figs 16–18 *Cyclothyris punfieldensis* sp. nov. (gerontic specimen). Upper Albian, Punfield Cove, Dorset. BB82341, × 1.

Figs 19–21 *Cyclothyris* sp. Belfast district, Northern Ireland. B8229, × 1½.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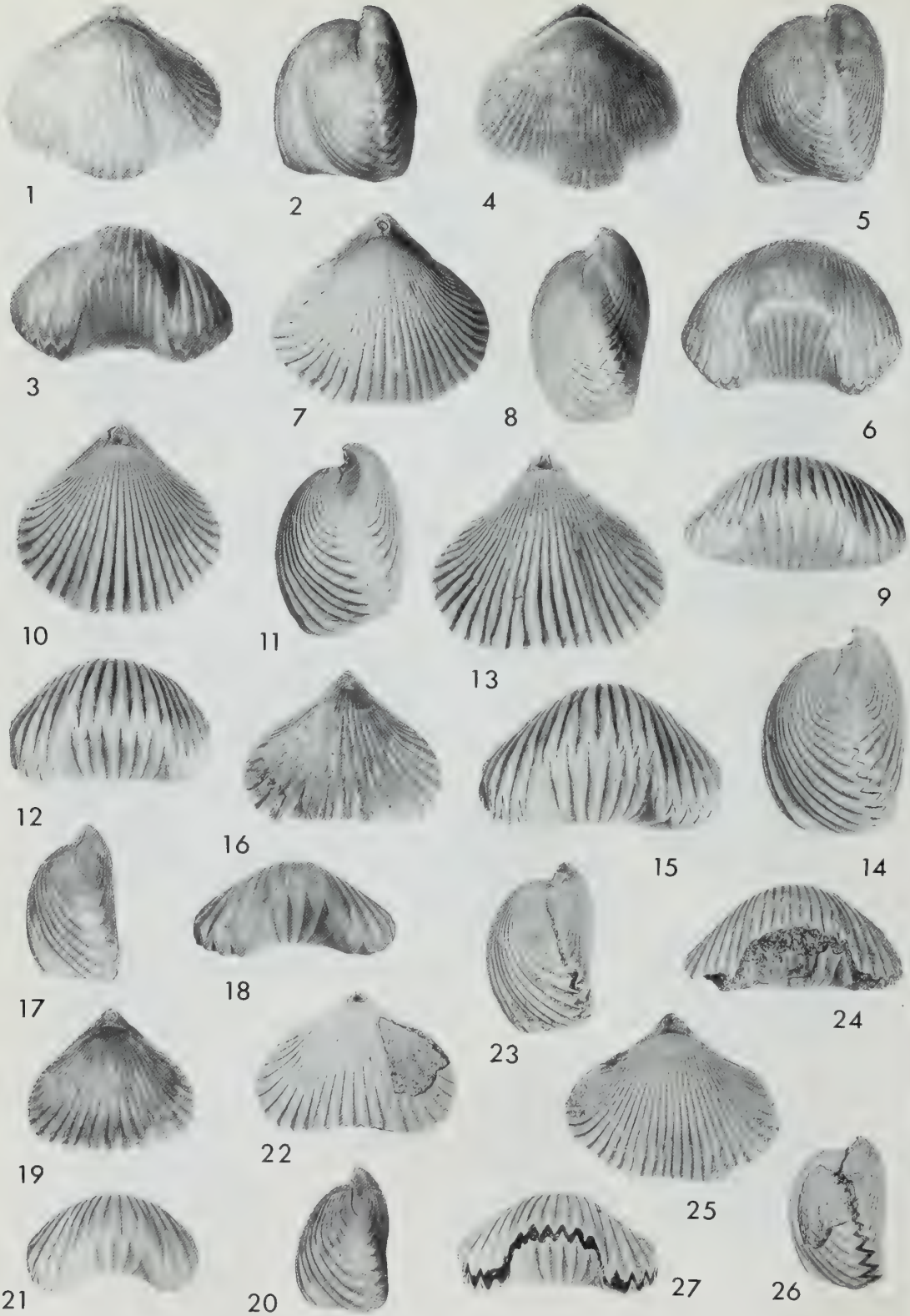
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characterize the Sables du Perche of the Upper Cenomanian in the Le Mans district (Sarthe), France, being distinct from related forms in both the Marnes à *Ostrea biauriculata* above and the Sables et Grès du Mans below. I now believe it to range through all three zones and to display variation in its valve thickening. The marginal thickening seen on valves of specimens collected from the Sables du Perche had been interpreted as a more generalized thickening of the valves, but is now thought to have resulted from local preservation, leaving the rest of the valve very much thinner. Comparison with material collected from other localities within the three Upper Cenomanian zones confirms the presence of the species in all three.

Specimens from Mayet (Sarthe) (Pl. 3, figs 22–27) have slightly more rounded costae, a less well defined triangular outline and a wider median fold and sulcus than those of *C. difformis* or *C. juigneti*.

Cyclothyris lamarckiana (d'Orbigny)
Pl. 3, figs 7–15

1849 *Rhynchonella lamarckiana* d'Orbigny: 32; pl. 496, figs 5–13.

Remarks. Originally described from the Cenomanian of the Le Mans district, the species characterizes the Marnes à Ostracées of the Briollay area (Sarthe). It is a comparatively large species with almost equal biconvexity of valves. The costae are strong and angular and average 30 on each valve, with about six anteriorly on the weak fold and about five in the low ventral sulcus and linguiform extension. There is a tendency to asymmetry of the anterior commissure, although this is not shown on the specimens figured here.

Dimensions of figured specimens. BB82203 (Pl. 3, figs 7–9): length 21·9 mm; width 24·9 mm; thickness 13·7 mm. BB82204 (Pl. 3, figs 10–12): length 21·3 mm; width 22·5 mm; thickness 14·0 mm. BB82205 (Pl. 3, figs 13–15): length 22·6 mm; width 25·7 mm; thickness 16·0 mm.

Genus *BURRIRHYNCHIA* Owen, 1962

Burrirhynchia devoniana sp. nov.
Pl. 1, figs 22–24

Diagnosis. Subtriangular to ovate *Burrirhynchia*, adults approximately 7·5 mm long, 6 mm wide and 10 mm thick. Strongly biconvex, uniplicate, dorsal fold low; linguiform extension trapezoidal, high. Shell surface multicostate. Hinge-teeth large: median septum low, no septalium.

Name. 'From Devon'.

Holotype. BB82252; from the Lower Cenomanian; White Hart sand pit, Wilmington, south Devon (Pl. 1, figs 22–24).

Other Material. In addition to the holotype about fifty specimens were studied. Paratypes are BB82253–9, BB76321, and SM B10289–93 from the type locality.

Description. Rarely specimens of *B. devoniana* from the White Hart sand pit show a tendency

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PLATE 3

Figs 1–6 *Cyclothyris formosa* sp. nov. Cenomanian, Lennier's Bed 10, St Jouin, Normandy. Figs 1–3, **Holotype** BB82206, × 1½. Figs 4–6, Paratype BB82207, × 1½.

Figs 7–15 *Cyclothyris lamarckiana* (d'Orbigny). Marnes à *Ostrea biauriculata*, Briollay, Sarthe. Figs 7–9, BB82203, × 1½. Figs 10–12, BB82204, × 1½. Figs 13–15, BB82205, × 1½.

Figs 16–21 *Cyclothyris juigneti* sp. nov. Cenomanian, *T. costatus* Zone, La Perrière (Orne). Figs 16–18, **Holotype** BB82208, × 1½. Figs 19–21, Paratype BB82209, × 1½.

Figs 22–27 *Cyclothyris compressa* (Valenciennes, *in* Lamarck). Upper Cenomanian, *naviculare* Zone, Marnes à *Ostrea biauriculata*, Mayet (Sarthe). Figs 22–24, BB82211, × 1½. Figs 25–27, BB82210, × 1½.

towards the typical sulciplicate sigmoid commissure of *B. sigma* (Schloenbach) from north Germany (see Schloenbach's drawing, 1867: pl. 23, figs, 5, 6). A broad sulciplication is also a feature of the type-species, *B. leightonensis* (Walker), from the Lower Albian of Leighton Buzzard, Bedfordshire (Pl. 1, figs 28–30).

Remarks. The chief differences between the Cenomanian *B. sigma* (Schloenbach) (1867: 500; pl. 23, figs 5–7) and *B. devoniana* is the costation, which in the former is fine and rounded in contrast to the fewer (20–25 on each valve with 6 in the sulcus) and more deeply incised ribs on *B. devoniana*. Variation is similar to that of the German species, but the outline is more elongate than in the Lower Albian *B. leightonensis*. It seems probable that the three species, *B. sigma*, *B. leightonensis* and *B. devoniana* are related and exhibit adaptations to different environments, manifested chiefly in the coarseness of their costation.

Subfamily **Uncertain**

Genus ***GRASIRHYNCHIA*** Owen, 1968

Grasirhynchia grasiana (d'Orbigny)
Pl. 5, figs 20–23

1849 *Rhynchonella grasiana* d'Orbigny: 38; pl. 497, figs 7–10.
1852 *Rhynchonella grasiana* d'Orbigny; Davidson: 96; pl. 12, figs 17–19.
1867 *Rhynchonella grasana* d'Orbigny (sic); Schloenbach: 496; pl. 2, figs 8, 9.
1878 *Rhynchonella grasana* d'Orbigny (sic); Deicke: 26, figs 20, 21.
1895 *Rhynchonella grasiana* d'Orbigny; Tiessen: 459.
1968 *Grasirhynchia grasiana* (d'Orbigny) Owen: 20; pl. 2, figs 7a, b, c.
1969 *Rhynchonella grasiana* d'Orbigny; Panow: 578; pl. 110, fig. 1.
1977 *Grasirhynchia grasiana* (d'Orbigny); Popiel-Barczyk: 36; pl. 3, figs 3–7; text-figs 10, 11.

Lectotype. Selected (Owen 1968) from 22 specimens in the d'Orbigny Collection, Museum d'Histoire Naturelle, Paris, No. 6497 in the d'Orbigny catalogue; from the Cenomanian of Le Havre, Normandy. Length 13·4 mm; width 15 mm; thickness 10 mm.

Remarks. The species, the type species of *Grasirhynchia*, was studied and redescribed (Owen 1968) using transverse serial sections of a British specimen from Sussex which had been carefully matched with the lectotype. Since then Popiel-Barczyk (1977) has published transverse sections through two specimens from the Lower Cenomanian of Annopol, Poland, comparable to those published by me in 1968. Of her figured sections those of 1977: fig. 10 most closely resemble my concept of the species.

The stratigraphical range of the species appears to be Lower to Middle Cenomanian. It exhibits a remarkable ecological tolerance and is found in various lithologies from highly glauconitic sandy limestones, such as the Upper Greensand of Warminster, Wiltshire and the Lower Cenomanian Limestone of Wilmington, Devon, to the more marly and chalky facies of the Middle Cenomanian in parts of Dorset, Sussex and Kent.

The species displays two size variants; the smaller and more finely costate specimens appearing to prefer the more highly calcareous and chalky facies of the western localities. Both forms, however, occur within the same beds. Further eastwards, in Sussex and Kent, larger, more coarsely costate specimens become more common, particularly within the marly chalk of the *rhotomagense* Zone in the coastal localities. Generally, the smaller form with finer costation is more strongly convex, having a domed dorsal valve and a moderately highly arched uniplicate fold. A broad shallow ventral sulcus is present anteriorly in all varieties.

The foramen is characteristically large for a small rhynchonellid, and is partially surrounded by auriculate extensions of the deltidium. This structure is not confined to *G. grasiana*, being present on well-preserved specimens of *G. martini* (Pl. 5, figs 24–26) and on some *Cyclothyris* specimens.

Geographically the species has a wide distribution, numerous examples having been collected from Wilmington, Whitecliff, Haldon Hills and Chardstock, Devon and from the Popple Bed at Mere, Wiltshire, to Melcombe Bingham, Dorset. A large, coarsely costate form has been

collected from Heytesbury and Chute Farm, Wiltshire. The species is not common on the Isle of Wight but examples have been obtained from the Glauconitic Marl of Compton Bay, Gore Cliff and Rocken End, Undercliff and Culver. A fine specimen was collected by Dr W. J. Kennedy from the Lower Cenomanian, *mantelli* Zone, *carcitanense* Subzone, west side of Woody Bay.

Continental collections have been made from the type locality and St Jouin in Normandy, from the more marly beds at Cran d'Escalles near Cap Blanc Nez as well as from Rougefort, Pas de Calais, Octerville and Vimoutier (Orne). One large specimen is said to come from the Basses Alpes in southern France; some nearly perfect examples were collected by Dr W. J. Kennedy from the Middle Cenomanian Sables de Lamnay, at a disused roadside pit near Courgenard, Sarthe.

Good examples resembling the lectotype were collected by Dr R. Marcinowski from the Lower Cenomanian of Czestochowa and Julianka in Poland. Other material from the Lower Cenomanian of Annopol is in the Museum Ziemi, Warsaw, Poland. The species occurs very rarely in beds considered to be of Middle Cenomanian age in Brochterbeck and Wunstorf, north Germany.

MATERIAL. The following list of British and some French examples in the BM(NH) is given with dimensions in mm.

Locality	length	width	thickness	BM(NH) No.
Warminster	11·7	13·3	10·4	2326
Chute Farm	9·4	10·7	6·8	98057
	10·8	11·4	7·3	„
	10·4	11·4	6·6	„
	9·2	9·8	6·5	„
	9·9	10·0	5·8	„
	9·1	9·5	7·9	„
	8·7	8·9	7·7	„
Chardstock	9·0	10·8	7·2	B8145
	9·6	8·9	7·7	„
	8·4	8·3	6·4	„
Undercliff, Isle of Wight	11·5	11·9	7·7	BB82371
	9·1	9·7	6·5	BB82372
Rougefort, Pas de Calais	9·0	8·5	6·8	–
	13·4	8·9	5·8	–
	12·1	7·9	6·2	–
	7·5	8·1	4·9	–

Grasirhynchia martini (Mantell)
Pl. 5, figs 24–26

1822 *Terebratula martini* Mantell: 31.
1826 *Terebratula pisum* J. de C. Sowerby: 70; pl. 536, figs 6, 7.
1838 *Terebratula pisum* Sowerby; von Buch: 148; pl. 15, fig. 18.
1852 *Rhynchonella martini* (Mantell) Davidson: 94; pl. 12, fig. 15 only.
1867 *Rhynchonella martini* (Mantell); Schloenbach: 499; pl. 23, fig. 10.
1895 *Rhynchonella martini* (Mantell); Tiessen: 458.
1968 *Grasirhynchia grasiana* (d'Orbigny) Owen: 20; pl. 2, figs 7a, b, c.

LECTOTYPE. B61480 in the Sowerby Collection; selected Owen (1968). Chalk Marl; Hamsey, Sussex (Pl. 5, figs 24–26).

REMARKS. This species is included here because confusion has arisen between examples identified as *G. martini* and specimens here assigned to *Monticlarella brevirostris* (Roemer), p. 103, originally described from the Pläner near Sarstedt, north Germany (Roemer 1840). Davidson

(1852) figured three specimens (his pl. 12, figs 15, 16a–d) of which one (fig. 15) is a true *G. martini*, while another (fig. 16a–c) is an example of *Monticlarella brevirostris* from the Chalk detritus of Charing, Kent. The third specimen (fig. 16d) is unrecognized but came from the Upper Greensand of Chute Farm, Warminster.

Monticlarella brevirostris (Roemer) is thought to be a senior synonym of *Rhynchonella rectifrons* Pictet from the Cretaceous (uncertain horizon) of Ste Croix, Vaud, Switzerland and is to be the subject of a future paper shared with C. J. Wood. In Britain it appears to be of stratigraphical significance, occurring at a restricted horizon within the Lower Chalk, and has been found with *G. martini* at Folkestone, Eastbourne and localities on the Isle of Wight.

Grasirhynchia martini is more ecologically limited than *G. grasiana* and appears to be restricted to the marly beds within the upper part of the Lower and the Middle Cenomanian. Records of its occurrence in the Lower Cenomanian sandy deposits in the Annopol district of Poland (Popiel-Barczyk 1977) are doubtful since her figured specimens (pl. 4, figs 1–3) may not be conspecific, although the serially sectioned specimen from Iwanowice (1977: fig. 12) belongs to *Grasirhynchia* and the sections are very like the series published earlier (Owen 1968: text-fig. 2) through a specimen from the Chalk Marl of Hamsey, Sussex.

MATERIAL. B25088, Lower Chalk, Heytesbury; B8139, Lower Chalk, Sussex (Davidson Collection); B8175, Pit 3, Hallington near Louth, Lincolnshire (J. F. Farmery Collection); one specimen from the Totternhoe Stone equivalent, Melton, Yorkshire (12/29, F. Whitham Collection, Hull).

Family **WELLERELLIDAE** Licharev, *in* Rzhonsnitskaya, 1959

Genus ***ORBIRHYNCHIA*** Pettitt, 1954

TYPE SPECIES. *Orbirhynchia orbignyi* Pettitt, 1954.

DISCUSSION. Pettitt (1954: 29) erected *Orbirhynchia* for his species *Orbirhynchia orbignyi*, from the Middle Chalk, Labiatus Zone, of Reigate, Surrey. He differentiated several species in the genus ranging from the Lower to Upper Chalk and attempted to distinguish his type species, *O. orbignyi*, from *O. cuvieri* by comparison of external morphology and type of costation. His distinctions are somewhat arbitrary, based on minor morphological differences which could be attributed to variation within the species, and this casts doubt upon the stratigraphical value of some of his taxa.

In my opinion, *O. cuvieri* from the Middle Chalk, and *O. wiesti* (Quenstedt) and *O. multicostata* Pettitt from the Lower Chalk, should be regarded as conspecific, while *O. compta* Pettitt and *O. orbignyi* are also possible synonyms of *O. cuvieri*.

Another group of *Orbirhynchia* species which appears to have many morphological characters in common is represented by *O. mantelliana* (J. de C. Sowerby) from the Lower Chalk, Chalk Marl of Hamsey, Sussex. This group can be distinguished from the *O. wiesti* group by its more robust appearance, flatter valves, coarser (fewer) costae and trapezoidal to asymmetrical anterior commissure. It also differs internally from the type species in having a thicker test and less well developed dental lamellae. I include the species *O. obscura* Pettitt, from the Lower Chalk of Folkestone, in synonymy with *O. mantelliana* as it appears to be nothing more than an intraspecific variant. *O. parva* Pettitt, from the Lower Chalk of Cambridge, is probably another synonym, but is consistently smaller and broader in general outline than the type specimen of *O. mantelliana* and may deserve subspecific status. *O. dispansa* Pettitt, from the Upper Chalk, appears to belong in the *mantelliana* group.

Orbirhynchia mantelliana (J. de C. Sowerby)

Figs 10–13; Pl. 4, figs 1–6, 10–12

1826 *Terebratula mantelliana* J. de C. Sowerby: pl. 537, fig. 5.
1838 *Terebratula mantelliana* Sow.; von Buch: 154; pl. 15, fig. 26.
1855 *Rhynchonella mantelliana* J. de C. Sowerby; Davidson: 87; pl. 12, figs 20, 21.

1954 *Orbirhynchia mantelliana* (J. de C. Sowerby) Pettitt: 31; pl. 3, figs 10a–c.
1954 *Orbirhynchia obscura* Pettitt: 35; pl. 3, figs 1a–c, 2a–c.
1969 *Orbirhynchia mantelliana* (J. de C. Sowerby); Kennedy: pl. 22, figs 5–7.

LECTOTYPE. Sowerby Collection, B61490; from the Lower Chalk of Hamsey, Sussex; selected Pettitt (1954). Pl. 4, figs 1–3.

DESCRIPTION. The species was adequately described by Pettitt (1954: 31), who gave the average dimensions as 12 mm long, 13 mm wide and 9 mm thick. The species is subpentagonal in outline and oval in anterior profile. The brachial valve is moderately convex with a slight but fairly broad fold anteriorly. The linguiform extension was described as broad with the anterior margin straight, but variants within the species tend to have an asymmetrical anterior commissure, a feature rarely found in other *Orbirhynchia* species. There are 12–18 comparatively deeply incised costae on each valve, with 4 on the fold and 3 in the sulcus.

INTERNAL CHARACTERS. The thickened shell, strong, partially fused dental lamellae and falcifer crura are shown in serial sections of a topotype by Pettitt (1954: fig. 10).

REMARKS. In spite of his recognition of material from Bedfordshire, Cambridgeshire, Kent, Surrey and Sussex, Pettitt's concept of the species appears to have been based largely upon the type specimen and comparatively few additional examples. The present study takes a somewhat broader view of the species, including variants from localities other than those already mentioned. A simple statistical analysis has been made from random samples obtained from these localities and a linear regression is presented here, Fig. 11. In addition, a pictograph illustrating the range of morphological variation is given, Fig. 12.

The species is regarded as an important stratigraphical marker and has been the subject of discussions by Jeans (1968) and Kennedy (1969). Kennedy emphasized the importance of an *Orbirhynchia mantelliana* Band within the *rhotomagense* Zone of the Middle Cenomanian in the southeast of England. He fixed the upper limit of his band as corresponding to the boundary between the *Turrilites costatus* and *T. acutus* assemblages, and in his correlation diagram (1969: fig. 16) he traced it across the Weald from Folkestone in Kent to Asham, near Beddingham, Sussex.

Recently, in an unpublished summary of research on Lower Chalk stratigraphy of the Sussex coast and inland areas, Helen Anderson (Brighton Polytechnic) has recognized another *Orbirhynchia mantelliana* band at Beachy Head, Eastbourne and Southerham Grey Pit, near Lewes, approximately 4 metres below that of Kennedy. It is not certain whether either of these bands can be directly equated with the *Orbirhynchia* Beds of Jeans (1968), but it seems likely

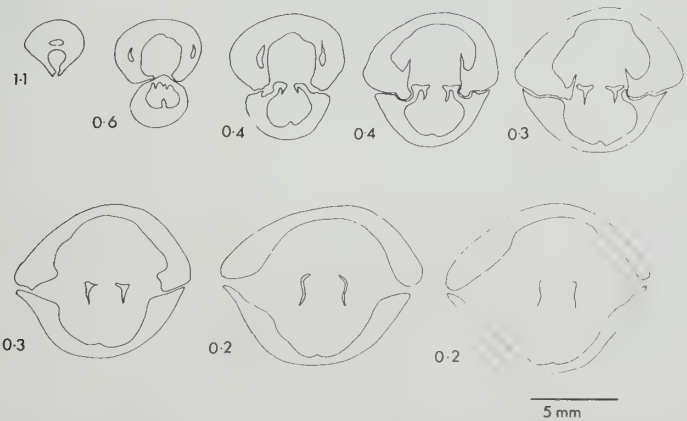


Fig. 10 *Orbirhynchia mantelliana* (J. de C. Sowerby). Transverse serial sections through a specimen (BB82355, Walker colln) from the Lower Chalk, Chalk Marl, of Hamsey, Sussex.

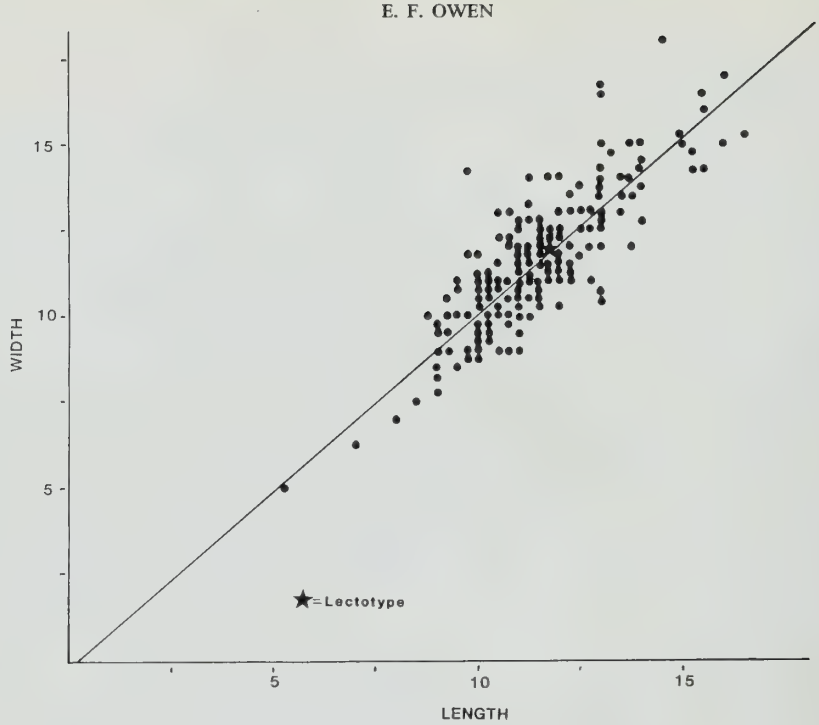


Fig. 11 Length × width graph and regression line for 159 specimens of *Orbirhynchia mantelliana* (J. de C. Sowerby) from England.

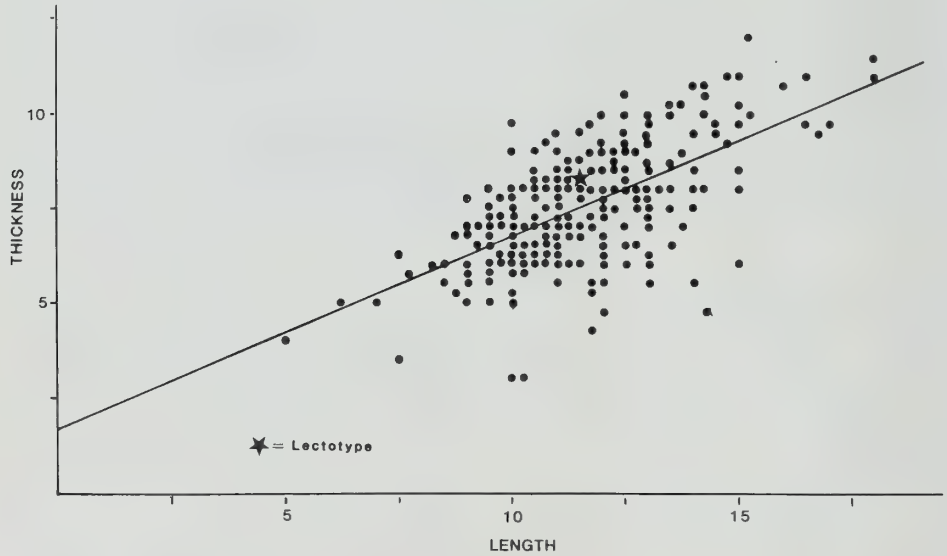


Fig. 12 Length × thickness graph and regression line for 159 specimens of *Orbirhynchia mantelliana* (J. de C. Sowerby) from England.

that the *O. mantelliana* specimens occurring in a band just above the Grey Bed, and at a level equivalent to Bed IV of Bower & Farmery (1910) within the *H. subglobosus* Zone in Lincolnshire and Yorkshire, might be the equivalent of the Upper *Orbirhynchia mantelliana* Band (Band 6 of Kennedy, 1969) which occurs in Sussex and Kent.

Schloenbach (1867: 494) described *Rhynchonella mantellana* [sic] from the *mantelli* and *rhotomagense* Zones of northwestern Germany, placing in synonymy Sowerby's original *Terebratula mantelliana* and Roemer's (1841) *T. paucicosta*. Schloenbach's figured specimen (pl. 23, fig. 11) shows a flatter form with a more circular outline and only slightly produced beak; his concept of *O. mantelliana* resembles only slightly the typical form which was, admittedly, rather poorly illustrated by Sowerby (1826). His specimen seems closer to Roemer's *T. paucicosta*, from the Essen Greensand, and could even have been a young form of that species. It also resembles a specimen figured by Panow (1969: 570; pl. 109, fig. 4) and another by Popiel-Barczyck (1977: 30; pl. 1, figs 7–9) called *Orbirhynchia mantelliana* from the Lower Cenomanian of Poland, which, in addition, have a more broadly arcuate anterior commissure than true *O. mantelliana*.

Many geographical and ecological variants have now been included within this species, largely because their separation can be seen to offer no stratigraphical advantage. The species is listed prominently from the Totternhoe Stone, or just above it, from the type area in Berkshire, southwards to Wiltshire and Dorset and as far north as Cambridge, Lincolnshire and Yorkshire. There are also examples which fall well within the present range of variation from Cran d'Escalles near Cap Blanc Nez, northern France and from Brochterbeck, north Germany. Specimens which can neither be included here, nor, so far as I can see, within *O. paucicosta*, occur in the Tourtia of Tournai, Belgium. This variant has also been collected from beds of a similar age at Montigny sur Roc, southern France. Specimens figured as *Rhynchonella mantelliana* by Deicke (1878) and Wanderer (1909) are also probably referable to *O. paucicosta* (Roemer).

Examples from the Totternhoe Stone at Burwell, Cambridgeshire, while clearly exhibiting all the typical morphological characters, almost always maintain a robust outline with acutely

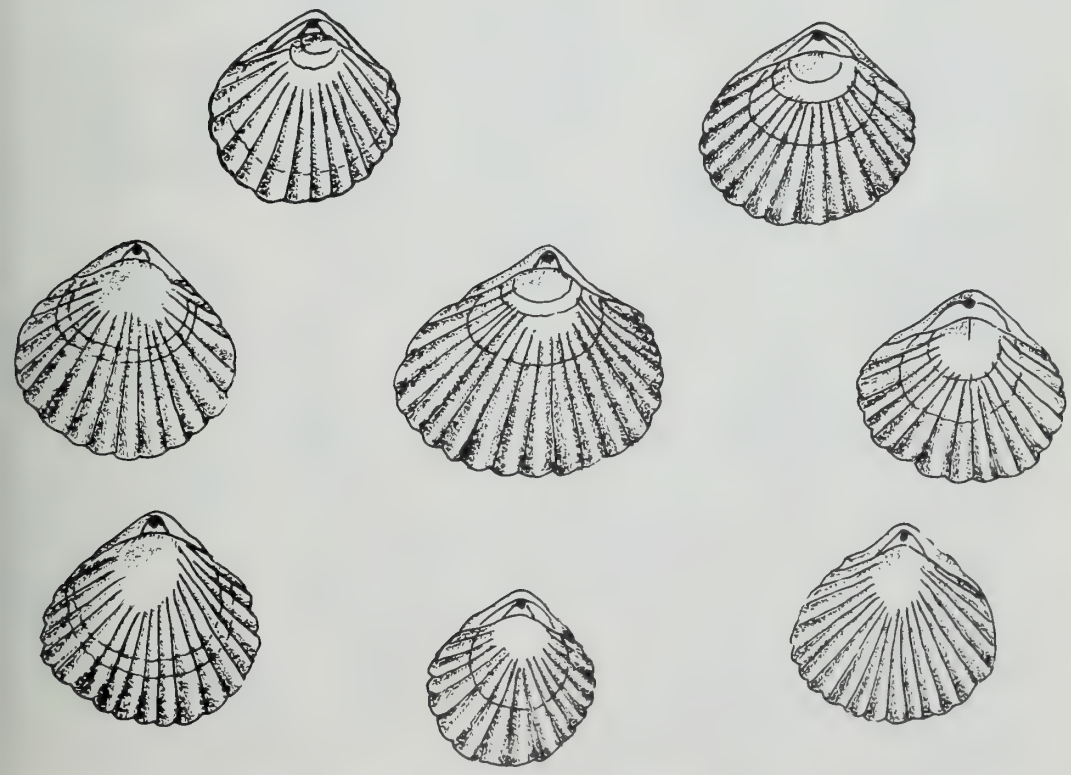


Fig. 13 Eight specimens showing the range of variation in *Orbirhynchia mantelliana*, from the Lower Chalk, *rhotomagense* Zone, Folkestone, Kent.

inflated valves and coarse, deeply incised costae; they are also larger (Pl. 4, figs 10–12). It is probable that this is the variant recorded by Bosworth (1906) in a band just above the Totternhoe Stone, which he called the *Rhynchonella mantelliana* Band, because of the abundance of large specimens of this species associated with '*Cidaris*' *dissimilis* and *Terebratulina nodulosa*.

MATERIAL AND DIMENSIONS. Because of the confusion surrounding this variable species I have presented both pictographic and statistical data. The following measurements are taken from a selection of specimens in the British Museum (Natural History) (prefix B or BB) and the British Geological Survey (others). Specimens in older collections may only have group registration numbers. Locality and stratigraphical details are quoted from the museum labels, but where possible checks have been made with colleagues from the B.G.S. Measurements in mm.

Number	length	width	thickness
Dover, Kent; *rhotomagense* Zone:			
B93747	15·9	15·0	10·3
B93750	13·4	13·6	8·0
BB37477	12·0	11·6	7·1
BB34478	11·0	11·1	8·8
BB34479	11·1	11·6	8·1
B22892	10·9	10·8	6·0
B93748	14·1	11·1	7·2
B93749	13·1	13·8	8·9
B93750	10·6	11·5	8·1
Margett's Pit, Burham, Kent:			
B44670	10·9	10·8	5·9
B44671	10·8	10·9	7·1
Folkestone, Kent; Grey Chalk:			
B25102			6·0
B25102	11·0	12·0	7·5
B25102	11·8	12·5	6·5
B25102	11·1	10·8	8·1
B25102	11·5	11·1	8·2
B25102	11·1	10·8	7·9
B25102	11·7	12·1	8·1
B25102	11·0	11·6	7·1
B25102	11·2	11·3	7·1
B25102	11·0	10·4	7·8

Number	length	width	thickness
Isleham, Cambridge:			
BGS 73064	13·1	12·9	9·9
73066	9·9	10·0	7·0
73067	9·9	10·0	6·5
73068	9·8	9·9	6·9
Norton Ferris, Wiltshire:			
Zb 968	15·2	17·0	11·0
969	14·0	16·2	10·5
970	12·1	13·1	7·1
971	12·9	13·4	8·9
972	13·0	13·9	9·2
973	13·0	13·9	9·9
974	12·5	14·3	8·0
975	12·0	12·4	7·9
Hitchin, Herts; Totternhoe Stone:			
37017	11·0	11·2	7·8
37019	12·8	12·9	8·3
Swaffam Prior, Cambridge:			
109617	10·0	9·9	7·5
109618	13·9	13·5	9·2

PLATE 4

Figs 1–6, 10–12 *Orbirhynchia mantelliana* (J. de C. Sowerby). Figs 1–3, Chalk Marl, Hamsey, E. Sussex. Lectotype B61490, × 1½. Figs 4–6, variant from Lower Chalk, *rhotomagense* Zone, Folkestone, Kent. B25105, × 1½. Figs 10–12, Totternhoe Stone, Barrington, Cambridge. BB81020, × 1½.

Figs 7–9 *Orbirhynchia* cf. *mantelliana* (J. de C. Sowerby) (?*paucicosta* Roemer). Lower Cenomanian, Le Mans district, Sarthe. BB82337, × 1½.

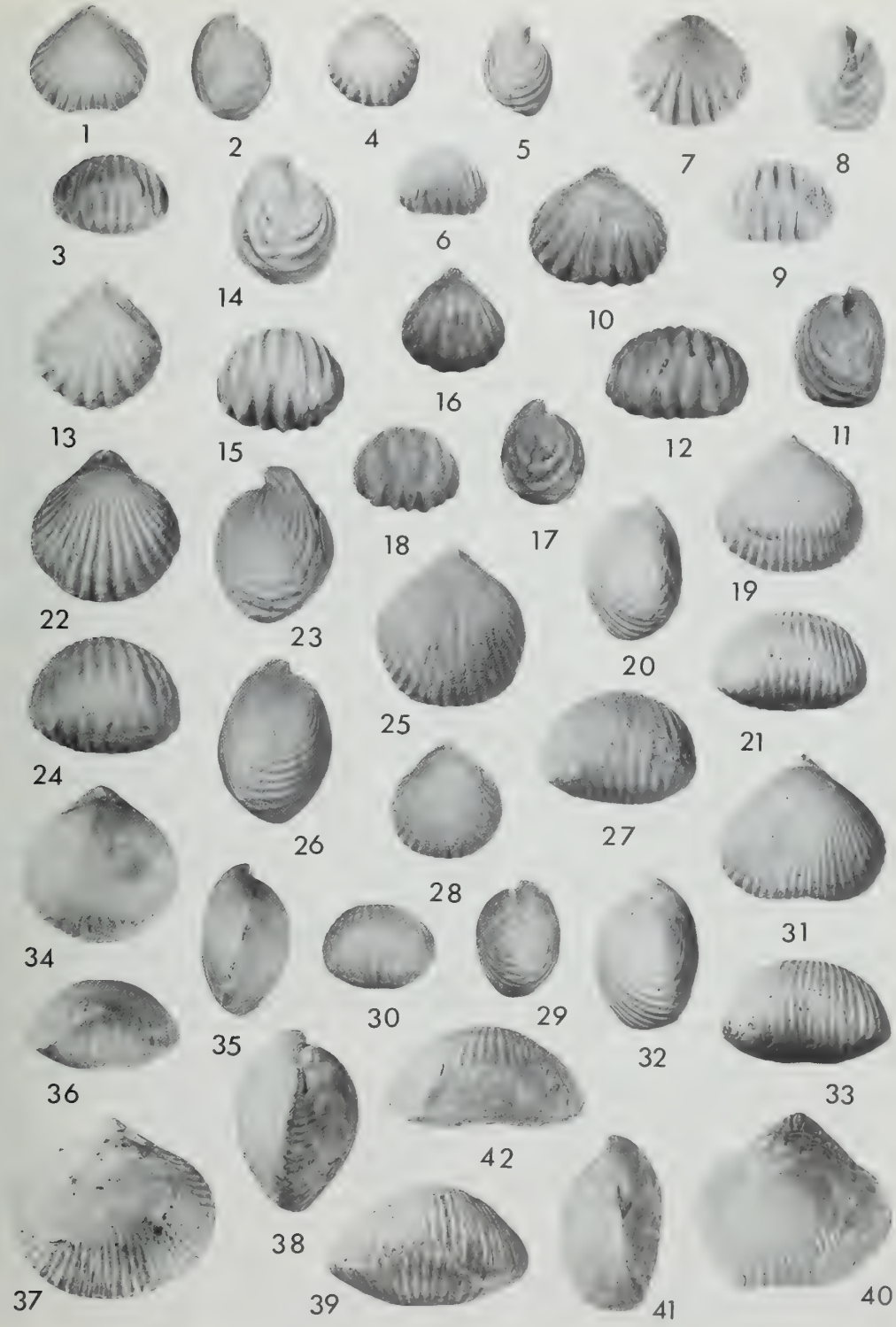
Figs 13–18 *Orbirhynchia wilmingtonensis* sp. nov. Figs 13–15, Craie de Rouen, Côte de Ste Catharine, Rouen. BB82338, × 1½. Figs 16–18, Lower Cenomanian, *mantelli* Zone, Wilmington, Devon. **Holotype** BB82132, × 1½.

Figs 19–21, 31–33 *Orbirhynchia boussensis* sp. nov. Upper Cenomanian, Sable de Bousse, Bousse (Sarthe), France. Figs 19–21, **Holotype** BB82131, × 1½. Figs 31–33, Paratype BB61140, × 1½.

Figs 22–24 *Orbirhynchia* sp. Red Rock, Hunstanton, Norfolk. B19904, × 1½.

Figs 25–30 *Orbirhynchia wiesti* (Quenstedt). Figs 25–27, Cenomanian, Bed B, Little Beach, Beer, Devon. BB7126, × 1½. Figs 28–30, Cenomanian Basement Bed, *naviculare* Zone, Askerswell, Dorset. BB82097, × 1½.

Figs 34–42 *Orbirhynchia multicostata* Pettitt. Upper Cenomanian. Figs 34–36, Plenus Subzone, South Ferriby. BB82342, × 1½. Figs 37–39, Plenus Marl, Marham, Norfolk. BB82343, × 1½. Figs 40–42, Plenus Marl, Burwell, near Louth, Lincolnshire. BB82344, × 1½.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These and measurements of other specimens from the Sedgwick Museum are included in the statistical analysis, the plots of which are given in Figs 11–12.

Orbirhynchia wiesti (Quenstedt)
Pl. 4, figs 25–30

1871 *Terebratula wiesti* Quenstedt: 166; pl. 41, fig. 54.
1874 *Rhynchonella wiesti* (Quenstedt) Davidson: 66; pl. 8, figs 31, a.
1896 *Rhynchonella wiesti* (Quenstedt); Jukes-Browne & Hill: 147.
1954 *Orbirhynchia wiesti* (Quenstedt) Pettitt: 37; pl. 3, figs 14a–c, 18a–c.
1962 *Orbirhynchia wiesti* (Quenstedt); Jefferies: pl. 77, fig. 32.
1970 *Orbirhynchia compta* Pettitt; Kennedy: 645.

LECTOTYPE. Selected by Pettitt (1954) from three specimens figured by Quenstedt (1871: pl. 41, fig. 54); from the Lower Chalk of Chardstock, Devon, and now in the Geologisches Paläontologisches Institut, University of Tübigen, Germany. Length 14·3 mm; width 12·3 mm; thickness 10·6 mm.

REMARKS. Pettitt recorded this species from Beer Head, Hooken Cliff and Chardstock in Devon, a distribution based on twenty specimens from museum collections. He restricted the species to those with only 28 costae and rejected Davidson's (1874) broader definition in which were included specimens with a total of 30 to 32 ribs. Jukes-Browne & Hill (1896) considered that Davidson's definition was too narrow: 'It is a much more variable species than Davidson seems to have supposed—the average number of ribs seems to be between 24–26, but there are many forms which have as few as 18, and others which have as many as 30; the former resemble *Rhynchonella mantelliana* except that the ribs are not so angular, and the latter come so near to the broader varieties of *R. cuvieri* that when placed beside them, they are indistinguishable.'

Pettitt (1954: 31) appears to have accepted these remarks in a general sense, but I think that Jukes-Browne & Hill were actually referring specifically to specimens from Bed 13 of Meyer (1874) which, they appear to be claiming, were all of one species.

The situation is somewhat analogous to the position of *O. mantelliana* where the typical Sowerby definition has been obscured by the numerous varieties added to the species. Before 1954, when Pettitt figured his lectotype of *R. wiesti*, the species could only have been interpreted from the illustrations of Quenstedt (1871: pl. 41, figs 52–54) and the specimen figured by Davidson (1874: pl. 8, fig. 31). It is not surprising, therefore, that the interpretation of Jukes-Browne & Hill (1896) should agree with forms from Bed C of the Cenomanian which are now thought to include variants of both *O. wiesti* and *O. multicostata*.

Jefferies (1962), in dividing certain faunal groups into cold water and warm water inhabitants, placed *Orbirhynchia multicostata* Pettitt into the cold water group and a specimen he identified as *O. wiesti* (pl. 77, figs 2a, 2b), belonging to neither the cold water nor the warm water group, was placed in a miscellaneous group. In his diagram of the standard succession at Merstham, Surrey, Jefferies (1962: 611) marked the point, Beds 7–8 within what was at that time the *Metoicoceras gourdoni* Zone, where *O. wiesti* commonly occurs. He also indicated a position, Bed 1, the *Metoicoceras geslinianum* Zone, where *O. multicostata* (p. 99) was said to be common. The relative position of these species in the *Actinocamax plenus* Subzone was said by Jefferies to be maintained throughout the entire Anglo-Paris Basin. However, the justification for Jefferies' two zones has been questioned by Kennedy & Hancock (1978, *in* Rawson *et al.*), and Wright & Kennedy (1981) have since suggested that the top part of the Upper Cenomanian be known as the *Neocardioceras juddi* Zone so both brachiopod species occur in this new zone.

If, as Jefferies suggested, *O. wiesti* lived in a completely different environment and temperature from that of *O. multicostata*, it is surprising to find Smith (1957a, b, 1961) recording both species within a comparatively narrow horizon, Bed C of Jukes-Browne & Hill (1896, 1903) on the south Devon coast. This might be explained by the condensed nature of the bed,

since Wright & Kennedy (1981: 8) regard it as the equivalent of the Plenus Marls and the top of the Cenomanian.

The species is recorded from the base of Bed 6 at Bovey Lane sand pit by Smith (1961: 117). The correlation of Bed 6 with Bed C of the coastal section was confirmed by Kennedy (1970: 660), who cited *O. multicostata* with *O. wiesti* and *Arcuatothyris rugulosa*. Specimens collected from this pit, identified as *O. wiesti*, vary in their broader and flatter valves, and slightly more produced umbo. *O. wiesti* has also been recorded from Bed 13 (Meyer 1874; Jukes-Browne & Hill 1896), where it is exceedingly rare.

Specimens have been studied in the British Museum (Natural History), including two from Bed B, Little Beach, Beer, Devon, and six from Bed C, Hooken Cliff (included in series BB76345–54). A typical form is in the Davidson Collection (BB12396), and is said to have come from the Glauconitic Marl of Chardstock. A range of variants came from the Chalk Basement Bed of Askerswell (BB7127–30).

Orbirhynchia multicostata Pettitt
Pl. 4, figs 34–42

1874 *Rhynchonella wiesti* Quenstedt; Davidson: 66; pl. 8, figs 31, a, b.
1903 *Rhynchonella wiesti* Quenst.; Jukes-Browne & Hill: 136, *in part*.
1954 *Orbirhynchia multicostata* Pettitt: 38; pl. 3, figs 20a, b.
1962 *Orbirhynchia multicostata* Pettitt; Jefferies: pl. 77, figs 2a, b.
1963 *Orbirhynchia multicostata* Pettitt; Jefferies: 7–18.

LECTOTYPE. Selected by Pettitt (1954) and one of two specimens figured by him (pl. 3, figs 20a, b) from the Upper Cenomanian, Plenus Subzone; Betchworth, Surrey. British Geological Survey, GSM 92642.

REMARKS. Pettitt (1954: 38) based the description of this species on two rather poorly preserved syntypes and mentioned a further ten specimens from the Subglobosus and Labiatus Zones and the Plenus Subzone of the Lower Chalk in Bedfordshire, Buckinghamshire, Cambridgeshire, Surrey and Sussex.

Since its original description, the species has been widely quoted from the Plenus Subzone in southeastern and eastern England and from beds considered to be of equivalent age in south Devon and Dorset. As a result, the interpretation of the species now includes many variants, which Pettitt might well have regarded as being outside his original concept. These forms range morphologically from subcircular to broadly oval in outline, with a short suberect beak and wide arcuate anterior commissure. A prominent concentric growth-line is commonly present at about half, or just anterior of half, the length of the shell.

In his original description of the Plenus Subzone of the Anglo-Paris Basin, Jefferies (1962) wrote that *O. multicostata* was a common fossil in Beds 1a and 1b of the standard succession of Merstham, Surrey, and also pointed out the apparently wide geographical distribution of this brachiopod in Britain and France at approximately the same horizon. He interpreted the spread of *O. multicostata*, which he thought originated from an early ancestor at Cap d'Antifer, as influenced by a shallowing of the outer reaches of the basin; this would probably also account for the rare occurrence of *Monticlarella jefferiesi* (formerly quoted as '*Rhynchonella*' *lineolata carteri*). The rise in temperature during the succeeding deposition in Bed 2, however, probably resulted in a reversal of the situation, when *M. jefferiesi* became comparatively common and *O. multicostata* exceedingly rare. The association of *O. multicostata* with the obviously shallow water brachiopod *Lingula* sp. appears to confirm the presence of shallow water conditions at Bed 1 level, as suggested by Jefferies (1962).

This species exhibits a greater tolerance to ecological variation than any *Orbirhynchia* species so far investigated. It appears in marls, limestones and chalky facies without significant variation. Throughout its extraordinary environmental range it maintains the same robust morphological features which must have inspired its separation from other species of the same genus at

PLATE 5

Figs 1–6, 13–15 *Terebratulina protostriatula* sp. nov. Figs 1–3, Chalk Marl, Hamsey, E. Sussex. **Holotype** BB6038, × $1\frac{1}{2}$. Figs 4–6, Lower Cenomanian, White Hart sand pit, Wilmington, Devon. Paratype BB82261, × $1\frac{1}{2}$. Figs 13–15, Essen Greensand, Essen, north Germany. B35690, × $1\frac{1}{2}$.

Figs 7–9 *Terebratulina striatula* (Mantell). Upper Chalk, Hamsey, E. Sussex. Holotype B457, × $1\frac{1}{2}$. See also Pl. 20, fig. 3.

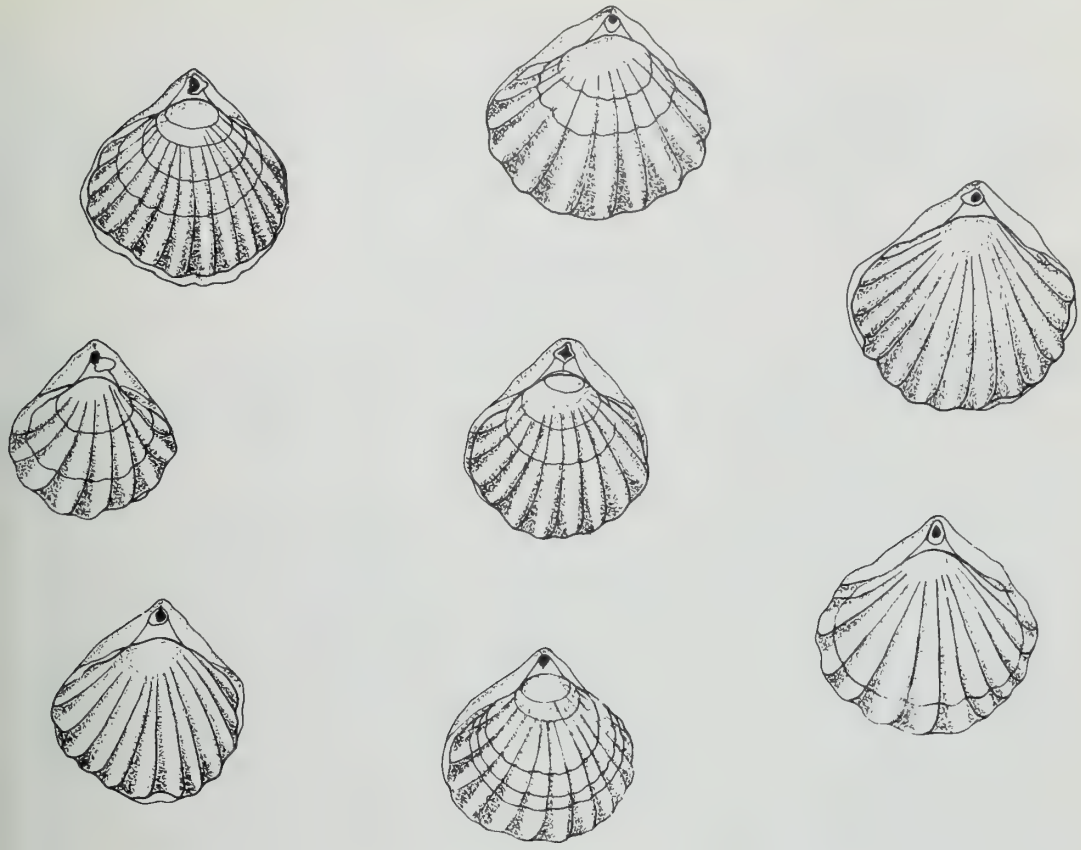

Fig. 14 Eight specimens showing the range of variation in *Orbirhynchia wilmingtonensis* sp. nov., from the Lower Cenomanian, White Hart sand pit, Wilmington, Devon.

the time of its description, although the specimens chosen for figuring by Pettitt do little to distinguish it clearly from *O. cuvieri* or *O. wiesti.*

Although from the literature this species does not appear to have been as widely distributed on the Continent as in the United Kingdom, Jefferies (1963) pointed out its value as a marker fossil in Bed 1 from Cap Blanc Nez and other northern French localities to Cap d'Antifer on

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Figs 10–12 *Terebratulina* ? *auriculata* (Roemer). Tourtia, Tournai, Belgium. B35491, × $1\frac{1}{2}$.
Fig. 16 *Terebratulina nodulosa* Etheridge. Red Rock, Bed A, Hunstanton, Norfolk. BB82368, × 4.
Fig. 17 *Terebratulina etheridgei* nom. nov. Cambridge Greensand, Cambridge. BB82369, × 4.
Figs 18–19 *Thecidiopsis essensis* Backhaus. Essen Greensand, Essen, north Germany. B5190, × 10.
Figs 20–23. *Grasirhynchia grasiana* (d'Orbigny). Cenomanian, Le Havre. Figs 20–22, Lectotype, Coll. Inst. de Pal., Paris No. 6497, × 2. Fig. 23, specimen showing characteristic auriculation of the foramen by the extension of the deltidial plates. BB84908, × 6.
Figs 24–26 *Grasirhynchia martini* (Mantell). Cenomanian, Chalk Marl, Hamsey, E. Sussex. Lectotype B61480, × 3.
Fig. 27 '*Argyrotheca*' *megatrema* (J. de C. Sowerby). Cambridge Greensand, Cambridge. BB6097, × 4.
Fig. 28 '*Argyotheca*' sp. Cenomanian, Essen Greensand, Essen, north Germany. B7218, × 4.
Figs 29–31 *Monticlarella carteri* (Davidson). Cambridge Greensand, Cambridge. BB44427, × $2\frac{1}{2}$.
Fig. 32 *Lingula subovalis* Davidson. Upper Greensand, Potterne, Wiltshire. B8291, × $1\frac{1}{2}$.

the coast, and it has been collected in beds of the same age at Cernay-en-Dormois east of the Paris Basin.

It is possible that the *Orbirhynchia* commonly found in the Sables de Bousse, Sarthe, may be a geographical variant of this species, but it maintains a uniformity of shape and size, and its umbonal characters distinguish it from the typical *O. multicostata*, so I describe it as a new separate species, *O. boussensis* (p. 103). Specimens from Bed C at Bovey Lane, Devon closely resemble *O. multicostata* and are probably a local variant of that species.

Orbirhynchia wilmingtonensis sp. nov.
Fig. 14; Pl. 4, figs 13–18

1852 *Rhynchonella mantelliana* Sow.; Davidson: pl. 12, fig. 22.
1903 *Rhynchonella mantelliana* Sow.; Jukes-Browne & Hill: 129.
Orbirhynchia mantelliana auctt.

DIAGNOSIS. Distinctly subcircular to triangular in outline. Strongly biconvex, coarsely costate. Umbo slightly produced, deltidium exposed. Anterior profile almost circular, anterior commissure uniplicate with high arch.

NAME. 'From Wilmington'.

DESCRIPTION. The costae on both valves are triangular in section and deeply incised. They vary from 10 to 12 in all, with two or three on the almost imperceptible dorsal median fold and with a corresponding number in the comparatively deep, anteriorly developed broad sulcus.

Variants have a more circular outline, slightly flatter valves and more prominent umbo. The species is quite distinct from *Orbirhynchia mantelliana* (J. de C. Sowerby) with which it has been confused in the past. The new species differs in having fewer and more deeply incised costae, more triangular outline and stronger biconvexity. It also has a produced umbo exposing the deltidium, a feature not often seen in other species of the genus. These features also distinguish it from *O. wiesti* and *O. multicostata*, both of which have more numerous and less deeply incised costae and a less protruding umbo.

HOLOTYPE. BB82132, from the Lower Cenomanian *Mantelliceras mantelli* Zone; White Hart sand pit, Wilmington, Devon. Length 11·6 mm; width 11·4 mm; thickness 9·4 mm. Pl. 4, figs 16–18.

OTHER MATERIAL. Numerous specimens in the British Museum (Natural History) from the type locality only. Paratypes are BB82133–43: for dimensions see below. The species is at present known only from south Devon.

REMARKS. Although the species has been referred to *O. mantelliana* by various authors, it compares more readily with a similarly robust form occurring in the Craie de Rouen and possibly also from the Lower Cenomanian of the Sarthe. The French specimens, however, are consistently more circular in outline and have a less marked anterior sulcus than the Devon species.

In its small number of costae *O. wilmingtonensis* resembles *T. paucicostata* Roemer from the Essen Greensand. The new species compares with Roemer's illustrations (1841: pl. 7, fig. 6), but his type material is missing, probably destroyed during World War II, and I have never seen a similar specimen from any locality in the German Cenomanian. There is, therefore, no evidence for Roemer's original concept of *O. paucicostata*. But a specimen figured by Quenstedt (1871: pl. 41, figs 24–26), from the Pläner, Essen, may have been compared with Roemer's type specimen and is probably typical of the species. It represents an uncommon species from the Greensand at Kassenberg and other localities in the north German Cenomanian. It differs from *O. wilmingtonensis* in its considerably smaller size, more circular outline and less produced umbo. Three further specimens from the Essen Greensand, which also might represent Roemer's species, are in the Bruckmann Collection, B15468. They are flatter than the specimen figured by Roemer (1841) and have a closer resemblance to *O. mantelliana* (J. de C. Sow.).

DIMENSIONS of paratypes in the BM(NH). Measurements in mm.

Number	length	width	thickness	Number	length	width	thickness
BB82133	12·6	12·0	8·5	BB82139	10·5	10·7	7·2
BB82134	14·1	13·2	10·5	BB82140	11·4	10·3	7·4
BB82135	11·6	11·4	9·1	BB82141	11·6	10·7	9·4
BB82136	12·3	12·0	9·3	BB82142	11·4	9·8	8·5
BB82137	12·9	11·8	8·9	BB82143	10·6	9·7	6·6
BB82138	11·2	11·4	8·9				

Orbirhynchia boussensis sp. nov.
Pl. 4, figs 19–21, 31–33

DIAGNOSIS. Comparatively large *Orbirhynchia*, subcircular to broadly triangular in outline. Umbo slightly produced, beak suberect, pointed. Foramen small surrounded by lateral extensions of the deltidium.

NAME. 'From Bousse'.

DESCRIPTION. The anterior profile is characteristically oval, with an arcuate uniplicate commissure. There is no dorsal fold and the sulcus is confined anteriorly. Adult variation extends only to minor differences in the width of shells. About 26–28 rounded or subangular costae ornament each valve, commonly with 9 in the sulcus, although up to 12 have been recorded. Some specimens have a strong growth-line at about half to two-thirds of their valve length.

HOLOTYPE. W. J. Kennedy Collection, BB82131; from the Upper Cenomanian, Sables de Bousse, Sables à *Catopygus obtusus*; in a disused pit 180 metres west of Cemetery, SW of Bousse, Sarthe, France (loc. 12 of Jefferies, 1963). Length 15·0 mm; width 15·9 mm; thickness 10·2 mm. Pl. 4, figs 19–21.

PARATYPES. BB61121–59, K. Evans Collection. Some dimensions are given below.

REMARKS. The species is unknown in Britain, although specimens in Bed C at Bovey Lane, Devon, considered here as local variants of *O. multicostata* Pettitt, resemble *O. boussensis*. The latter can be distinguished by its more evenly biconvex profile, more massive beak, higher uniplication and from the Devon specimens by its less transverse outline; it somewhat resembles specimens from the Plenus Subzone of Lincolnshire.

DIMENSIONS of some paratypes. Measurements in mm.

Number	length	width	thickness	Number	length	width	thickness
BB61140	15·2	16·8	11·3	BB61144	13·3	15·5	10·9
BB61141	15·3	16·2	11·7	BB61145	15·2	16·8	10·6
BB61142	14·1	15·7	10·7	BB61146	13·5	16·5	10·5
BB61143	13·8	16·2	10·2				

Family **NORELLIDAE** Ager, 1959

Subfamily **MONTICLARELLINAE** Childs, 1959

Genus ***MONTICLARELLA*** Wisniewska, 1932

Monticlarella brevirostris (Roemer)
Pl. 18, fig. 4.

1840 *Terebratula brevirostris* Roemer: 41; pl. 7, fig. 7.
1852 *Rhynchonella martini* Mantell; Davidson: pl. 12, figs 16, 16a–d.

REMARKS. This species is thought to be of stratigraphical importance and is being investigated with C. J. Wood. It resembles and has often been confused with *Grasirhynchia martini* (Mantell), p. 91, with which it is found in the Chalk Marl at Folkestone, Dover, Eastbourne,

and at Compton Bay and Rocken End on the Isle of Wight. Whether it occurs independently of *Grasirhynchia martini* is not known.

It differs from other *Monticlarella* species in having well developed costae and in lacking the parasulcate anterior commissure characteristic of *M. carteri* (Pl. 5, figs 29–31) and *M. jefferiesi*.

MATERIAL. Numerous specimens from the Chalk Marl, *rhotomagense* Zone of Folkestone and Dover, British Museum (Natural History).

Superfamily **TEREBRATULACEA** Gray, 1840

Family **TEREBRATULIDAE** Gray, 1840

Subfamily **SELLITHYRIDINAE** Muir-Wood, 1965

Genus ***SELLITHYRIS*** Middlemiss, 1959

Sellithyris tornacensis (d'Archaic)
Pl. 6, figs 1–3

1841 *Terebratula subundata* Phillips; Roemer: 42; pl. 7m, fig. 15.
1847 *Terebratula tornacensis* d'Archiac: 316; pl. 18, figs 3a–e, 4a, 5a–b.
1867 *Terebratula tornacensis* d'Archiac; Schloenbach: 438 (38); pl. 21 (1), figs 8, 8a.
1878 *Terebratula tornacensis* d'Archiac; Deike: 12, fig. 3a, b.
1929 *Rectithyris tornacensis* (d'Archiac) Sahni: 10.
1959 *Sellithyris tornacensis* (d'Archiac) Middlemiss: 113.

NEOTYPE. The original material, including *Terebratula tornacensis*, of d'Archiac's (1847) classic description of the brachiopod fauna of the Tourtia has been lost (Dr Annie Dhondt, personal communication). A neotype, from the Tourtia of Tournai, Belgium, B85066, matching the illustrations in d'Archiac (1847) is therefore selected. Length 30·0 mm; width 28·4 mm; thickness 18·3 mm. Pl. 6, figs 1–3.

OCCURRENCE. The species occurs comparatively rarely in the Essen Greensand at Kassenberg, north Germany, in the Sable et grès du Mans at Le Mans, and in the Sables du Perche, Broillay. The species may have been recorded as *Terebratula biplicata* Sowerby and *Sellithyris biplicata* from the hardground sequences of Orbiquet and Goneville, Normandy in the Craie Glauconieuse, and Juignet's (1974) record of *Sellithyris biplicata* from the above localities is correct. *S. tornacensis* also occurs in the greensand deposits at Aix-en-Gohelle, Artois (Parent 1893).

REMARKS. This is a distinctive species and was well described by Middlemiss (1959). Morphological variation amounts to a usually slightly more oval outline or less marked pentangulate aspect and less acute biplication of the anterior commissure than shown in d'Archiac's original figure (1847: pl. 18, figs 3, 4, 5). In the Sables du Mans and the Sables du Perche, where the species appears to be more prolific than in the Belgian type locality, and Essen Greensand, specimens tend towards a less truncated umbo and slightly more erect beak.

PLATE 6

Figs 1–3 *Sellithyris tornacensis* (d'Archiac). Tourtia, Tournai, Belgium. **Neotype,** herein selected, B85066, × 1½.
Figs 4–6 *Harmatosia crassa* (d'Archiac). Tourtia, Tournai, Belgium. BB84908, × 1½.
Figs 7–9 *Sellithyris phaseolina* (Valenciennes, *in* Lamarck). Cliff Section at Porte des Barques, Charente, France. BB82286, × 1½.
Figs 10–12 *Rectithyris wrightorum* sp. nov. Lower Cenomanian, *mantelli* Zone, White Hart sand pit, Wilmington, Devon. **Holotype** BB82175, × 1.
Figs 13–15 ? *Ornatothyris* sp. Grey/Red Chalk, Speeton Cliff, N. Yorkshire. BB82346, × 1½.
Figs 16–18 *Concinnithyris* cf. *subundata* (J. Sowerby). Culver Cliff, Isle of Wight. BB76462, × 1½.
Figs 19–21 '*Ornatothyris*' sp. Grey Chalk, Speeton, N. Yorkshire. BB43360, × 1½.
Figs 22–24 *Moutonithyris anglia* sp. nov. Bed C, Red Rock, Hunstanton, Norfolk. **Holotype** BB82262, × 1.

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DIMENSIONS of BM(NH) specimens. Measurements in mm.

Number and locality	length	width	thickness
B85067, Tournai	25·0	23·3	14·8
B85068 „	27·2	21·9	14·6
B85069 „	23·9	21·0	13·7
B85070 „	24·1	18·5	11·5
B85071 „	27·3	25·0	16·3
B85072 „	28·3	26·6	17·3
65485, Briollay (Sarthe)	27·4	24·6	15·9
„ „	27·0	25·1	15·6
„ „	28·0	26·2	16·8
„ „	24·7	23·5	16·0
„ „	22·7	22·8	13·7
„ „	23·8	22·9	14·0

Sellithyris phaseolina (Valenciennes, *in* Lamarck)
Pl. 6, figs 7–9; Pl. 18, figs 11–13

1819 *Terebratula phaseolina* Valenciennes, *in* Lamarck: 251, No. 29.
1850 *Terebratula phaseolina* Valenciennes, *in* Lamarck; Davidson: 439; pl. 13, fig. 29.
1910 *Terebratula phaseolina* Val. in Lm.; Clerc & Favre: pl. 6, figs 28–33.
1971 *Sellithyris biplicata* Gaspard: 1–10; pl. 1, figs 1a–7c; pl. 2, figs 1–6.

LECTOTYPE. The specimen figured by Clerc & Favre (1910: pl. 6, figs 33), one of the remaining four syntypes in the Lamarck Collection, Museum d'Histoire Naturelle, Geneva. Length 14·1 mm; width 12·4 mm; thickness 8·0 mm. Herein selected.

Like so many of the Lamarck species, there was neither clear indication of a type specimen nor illustration of the species. Davidson (1850: 439) attempted to establish the species by figuring a specimen from the Lamarck Collection, but this cannot be selected as lectotype because his drawing appears to have been made up from several of Lamarck's syntypes.

Clerc & Favre (1910: pl. 6, figs 28–33) catalogued eight specimens in the Lamarck Collection, figuring six which were identified as A–F. Examination of these six remaining *Terebratula phaseolina* specimens, in the Department of Geology, Museum d'Histoire Naturelle, Geneva, reveals that only four can be positively identified: pl. 6, fig. 29 = specimen A, fig. 30 = specimen C, fig. 31 = specimen D, and fig. 33 = specimen F, the lectotype.

REMARKS. At the type locality, Le Mans, large and smaller forms are found together in the sandy, less chalky, facies; the lectotype is of the smaller variety. This does not have the marked biplication or the elongated an inflated umbo of the larger form. Both varieties are recognized in collections from the Marnes à *O. biauriculata* of Briollay (Maine et Loire) and from beds in the *Metoicoceras gourdoni* Zone of Mézières sous Ballon (Sarthe).

DIMENSIONS of BM(NH) specimens. Measurements in mm.

Number	length	width	thickness	Number	length	width	thickness
Mayet (Sarthe):				Port des Barques:			
BB82280	17·3	16·1	8·8	BB82286	18·9	16·6	10·7
BB82281	18·5	16·8	10·9	BB82287	16·9	15·1	10·0
BB82282	18·2	16·4	9·7	BB82288	18·1	17·2	10·0
BB82283	17·0	14·9	9·3	BB82289	18·5	16·9	11·0
Mézières sous Ballon:							
BB82290	15·5	14·3	9·3				
BB82291	13·5	12·2	6·7				

Genus ***OVATATHYRIS*** nov.

TYPE SPECIES. *Terebratula ovata* J. Sowerby, 1812.

NAME. The name *Ovatothyris* appeared in a Ph.D. thesis by Dr Margaret Cox (University of London, 1967). Her diagnosis and description have been emended and the name altered to

Ovatathyris in order to agree with the species. Credit is due to Dr Cox for the recognition of this genus.

DIAGNOSIS. Outline oval, beak suberect, foramen large, circular, marginate, mesothyridid; beak ridges well defined. Symphytium short, well exposed. Anterior commissure sulcate to slightly paraplicate. Folding concentrated in anterior half of shell. Cardinal process low, tapering. Crural processes high, inwardly inclined. Transverse band moderately highly arched.

EMENDED DESCRIPTION. The low, flat cardinal process, seen in transverse serial sections of the two *Ovatathyris* species described here, is typical of species in the subfamily Sellithyridinae, as is the degree of concavity of the hinge-plates. It is noteworthy that the transverse band, while maintaining a fairly uniform breadth, is more highly arched than in *Musculina*, *Platythyris* or *Boubeithyris*.

Ovatathyris remained consistently oval during growth but developed a marked sulcus anteriorly on the dorsal valve which, in anteriorly carinate specimens, led to paraplication of the commissure.

REMARKS. *Ovatathyris* differs from *Boubeithyris* in having an oval outline, sharper beak-ridges, more highly developed and relatively more frequently occurring growth-lines, and shell ornament of short radiating spinules. It differs internally from *Boubeithyris* in having slightly longer and more acutely concave hinge-plates, and from *Walkerithyris* by the absence of piped hinge-plates and in having a sulciplicate to paraplicate anterior commissure.

The genus is represented only by the two species described herein. One of these, *Ovatathyris ovata*, occurs as a comparatively common fossil in the Lower Cenomanian, *Mantelliceras mantelli* Zone, of the Grizzle at Wilmington, south Devon and from the Glauconitic Marl of Warminster, Wiltshire. The other species, *Ovatathyris potternensis* sp. nov., also occurs in the Glauconitic Marl at Warminster and the type locality at Potterne, Wiltshire. A variant of *O. potternensis* occurs rarely in the highly fossiliferous beds within the Glauconitic Marl of the Isle of Wight.

Ovatathyris ovata (J. Sowerby)
Fig. 15; Pl. 7, figs 19–24; Pl. 25, figs 3–4

1812 *Terebratula ovata* J. Sowerby: 46; pl. 15, fig. 3.
1849 *Terebratula lacrymosa* d'Orbigny: 99; pl. 512, figs 6–11.
1852 *Terebratula ovata* Sowerby; Davidson: 47; pl. 4, figs 6–13.
1874 *Terebratula ovata* Sowerby; Davidson: 32; pl. 2, fig. 14.

DESCRIPTION. Oval in outline with a sulcate to paraplicate anterior commissure. The large, circular foramen truncates the massive suberect umbo, bounded by sharp beak-ridges, outlining a short triangular interarea. A shallow dorsal sulcus originates at about half the valve length and deepens and widens anteriorly. The pedicle valve is correspondingly carinate, a feature commonly originating at about one-third of the valve length, producing a greater convexity than in the brachial valve.

Shell ornament consists of step-like concentric growth-lines and short spinules which, however, may not be preserved. When examined under a hand lens it is seen that the short spinules are arranged along growth lines in pairs, unlike those of *Arcuatothyris* which are more widely scattered. The higher magnification offered by the electron microscope (Pl. 25, figs 3–4) shows the short, paired bases of the spinules on the surface of *O. ovata* from the Warminster district. Although Davidson described and illustrated these spinules on several specimens (1852: pl. 4, figs 6–13) their preservation is not always good, probably because of abrasion, and indeed they cannot be distinguished on the type specimen.

INTERNAL CHARACTERS. In transverse serial sections through a specimen from Warminster it can be seen, Fig. 15, that a pedicle collar was not developed in the ventral umbo and that a low, poorly developed cardinal process is present in section 3. The long, slender hinge-teeth first appear on section 4 and by sections 5 and 6 are deeply inserted into the brachial valve sockets.

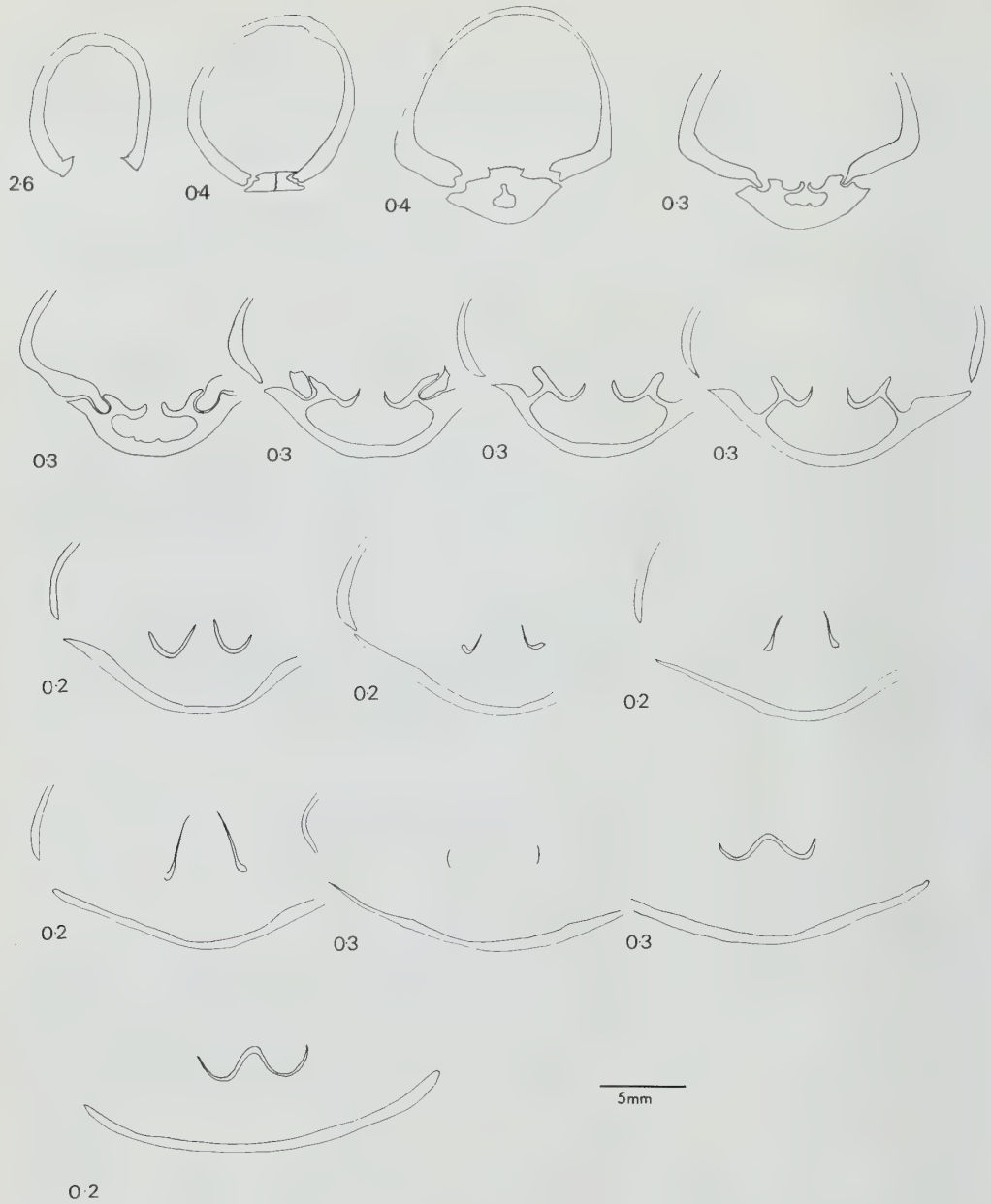


Fig. 15 *Ovatathyris ovata* (J. Sowerby). Fifteen transverse serial sections through 88764 from the Upper Greensand, Warminster, Wiltshire.

Acutely ventrally concave hinge plates, from which strong inner and outer socket ridges arose, become progressively U-shaped anteriorly. The crural processes are long and slender, curving gently towards one another. A highly-arched transverse band of the brachial loop occurs at about 6·5 mm from the ventral umbo.

HOLOTYPE. Sowerby Collection, B49840; from the Lower Chalk; Chute Farm, Wiltshire.

DIMENSIONS of BM(NH) specimens. Measurements in mm.

Number and locality	length	width	thickness
B492, Warminster	24·6	19·3	13·9
„ „	25·0	17·2	14·6
„ „	32·2	20·1	18·3
„ „	28·5	18·6	16·0
„ „	26·5	18·2	13·6
BB5534, south Wiltshire	32·4	25·5	18·1
B6297, Vimoutiers (Orne), France	33·8	24·4	18·1

REMARKS. The species is well known from the Warminster and Wilmington localities, but occurs also in Bed A of the Cenomanian Limestone at Chardstock, Devon (B1522); rarely from the Chalk Basement Bed, *acutus* Subzone of the *rhotomagense* Zone, Middle Cenomanian of Snowdon Hill, Chard (BB82219); the Lower Chalk, Basement Bed, Osmington, Dorset (BB82152) and from an unknown zone within the Cenomanian from Maiden Newton, Dorset, in the J. F. Walker Collection (B25279).

In France, *Ovatathyris ovata* occurs rarely in the coarse sandy beds and the glauconitic marls which crop out along the Normandy Coast from St Jouin to Cap de la Hève, where it has been called '*Terebratula*' *lacrymosa* d'Orbigny. Roemer's (1840: 44) record of *T. ovata* from this area is inaccurate.

O. ovata appears to be confined to the British and French Lower Chalk, but five specimens showing a similar outline, strongly sulcate to paraplicate anterior commissure and typical spinose ornament have been found in the Pictet Collection, Museum d'Histoire Naturelle, Geneva from Perte du Rhône, Switzerland (CB 8, 56–58, 89). These are compared to *O. ovata* and one is figured here (Pl. 7, figs 19–21).

Ovatathyris potternensis sp. nov.
Fig. 16; Pl. 7, figs 10–18; Pl. 25, figs 1–2

1847 *Terebratula squamosa* Mantell; Davidson & Morris: 254; pl. 18, fig. 8, a, b.
1852 *Terebratula squamosa* Mantell; Davidson: 50; pl. 5, figs 7–9.

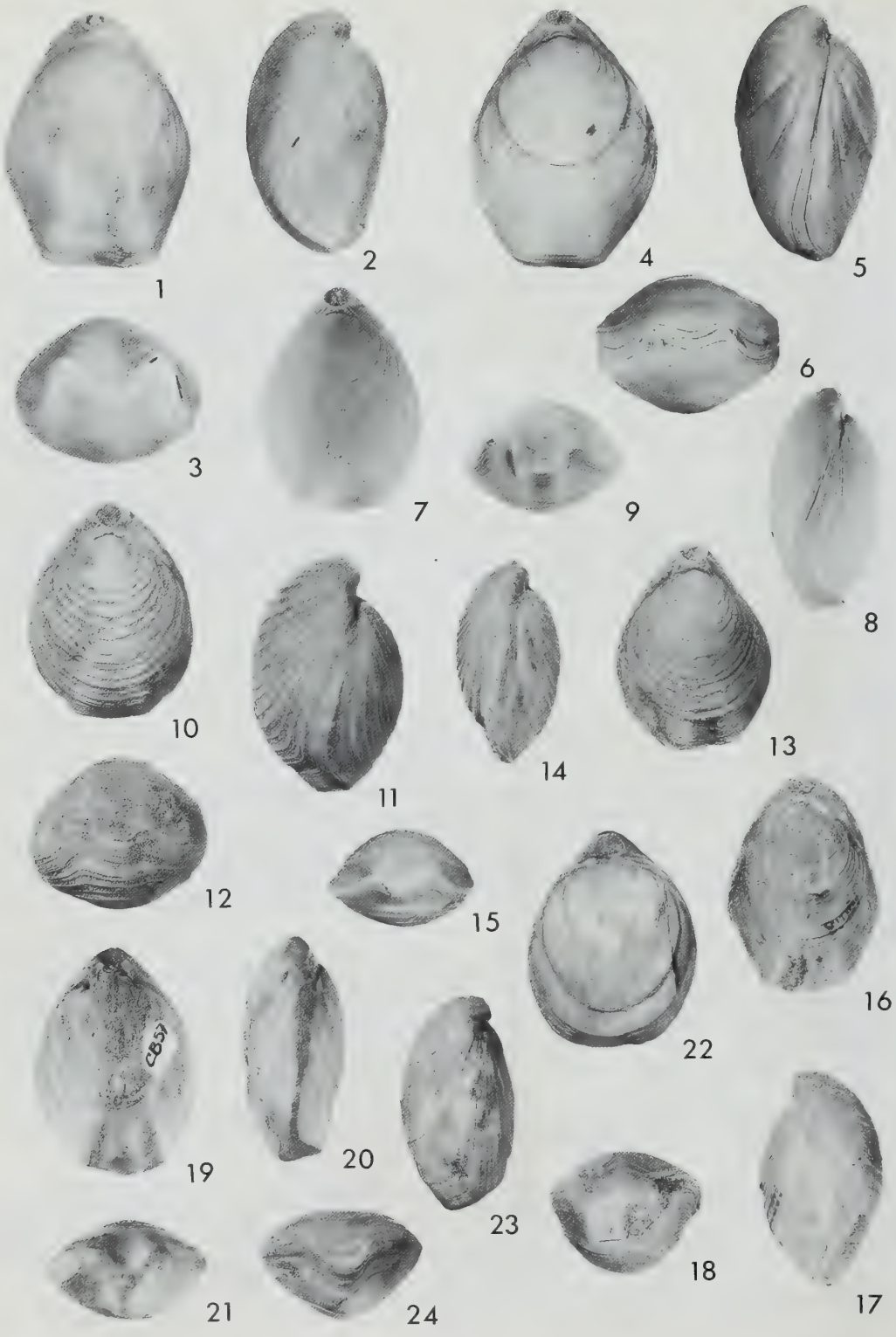
DIAGNOSIS. Biconvex *Ovatathyris*; pentagonal to oval in outline. Umbo massive, slightly produced, beak suberect, beak-ridges distinct. Interarea extensive, symphytium well exposed; foramen large, circular, mesothyridid. Biplicate to paraplicate. Rugose ornament.

NAME. 'From Potterne'.

DESCRIPTION. An ornament of short spinules, similar to those described for the type species, occurs on the lateral flanks of well preserved specimens. This can be seen using a light microscope but is best recorded using a scanning electron microscope (Pl. 25, figs 1–2, from examples of *O. potternensis*, compared with those from *O. ovata*, Pl. 25, figs 3–4). Serial sections (Fig. 16) compare closely with those taken through a specimen of *Ovatathyris ovata* from Warminster, Wiltshire.

HOLOTYPE. BB82149; from the Upper Greensand; Rifle Butts, Potterne, Wiltshire. Length 24·3 mm; width 18·7 mm; thickness 16·0 mm. Pl. 7, figs 10–12.

REMARKS. The rugose ornament of concentric growth-lines on this species led Davidson to believe that he was describing Mantell's *Terebratula squamosa* from the Chalk Marl of Hamsey, but a close study reveals that they lack the additional ornament seen on *T. squamosa*. Compare Pl. 25, figs 1–2 (*O. potternensis*) with Pl. 27, figs 1–4 (*Capillithyris squamosa*); see also Pl. 28, figs 1–4 (*C. disparilis*). *O. potternensis* also occurs in the Glauconitic Marl of Compton Bay, Isle of Wight.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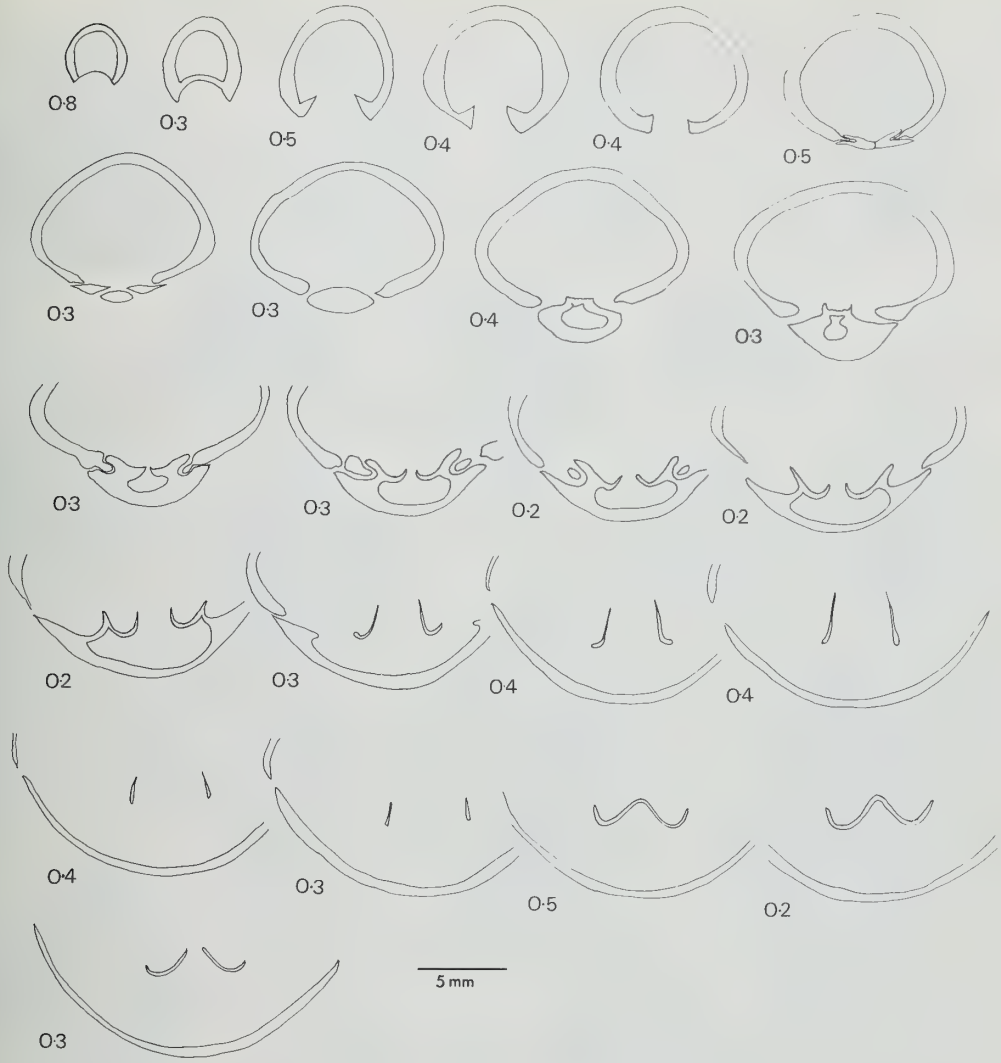


Fig. 16 *Ovatathyris potternensis* sp. nov. Twenty-three transverse serial sections through 88763 from the Upper Greensand of Potterne, Wiltshire.

PLATE 7

Figs 1–3 *Boubeithyris diploplicata* sp. nov. Lower Cenomanian, Vimoutiers (Orne), France. B6289, × 1.

Figs 4–9 *Boubeithyris boubei* (d'Archaic). Figs 4–6, Tourtia, Tournai, Belgium. BB82370, × 1. Figs 7–9, Lower Cenomanian, Le Havre, Normandy. B10816, × 1.

Figs 10–18 *Ovatathyris potternensis* sp. nov. Figs 10–12, Glauconitic Marl, Potterne, Wiltshire. **Holotype** BB82149, × 1. Figs 13–18, Glauconitic Marl, Compton Bay, Isle of Wight. Figs 13–15, BB59839, × 1. Figs 16–18, BB82189, × $1\frac{1}{2}$.

Figs 19–21 *Ovatathyris* cf. *ovata* (J. Sowerby). ? Upper Albian, Perte du Rhône, Switzerland. Geneva Museum (Nat. Hist.) coll. No. CB 57, × $1\frac{1}{2}$.

Figs 22–24 *Ovatathyris ovata* (J. Sowerby). Warminster Greensand, Warminster, Wiltshire. BB84902, × $1\frac{1}{2}$.

O. potternensis can be distinguished from *O. ovata* by its consistently acute biconvexity and its rugose shell ornament. It can be distinguished from other species of Terebratulidae, such as *Ornatothyris*, largely by its internal characters; also the acute ventrally concave hinge-plates and high arched transverse band of the brachial loop.

It seems likely that the species is confined to the Upper Greensand.

MATERIAL. Additional specimens from Potterne are in the Walker Collection (B25261, B25284), the Davidson Collection (B8287–9) and the C. W. & E. V. Wright Collection (BB82148); and 88763: Fig. 16. Also from the Isle of Wight (BB59839 and BB82189).

Genus ***BOUBEITHYRIS*** Cox & Middlemiss, 1978

TYPE SPECIES. *Terebratula boubei* d'Archiac, 1847.

Boubeithyris boubei (d'Archiac)
Pl. 7, figs 4–9

1847 *Terebratula boubei* d'Archiac: 320; pl. 19, fig. 11.
1903 *Terebratula boubei* d'Archiac; Lamplugh & Walker: 252; pl. 18, fig. 5.
1978 *Boubeithyris boubei* (d'Archiac); Cox & Middlemiss: 419; pl. 40, figs 1–4; text-fig. 4.

NEOTYPE. M.T.C. 10154, from the Tourtia of Tournai, Institut Royal des Sciences Naturelles de Belgique, Brussels. Selected Cox & Middlemiss, 1978.

REMARKS. Cox & Middlemiss (1978) recognized the species in the Lower Albian of Leighton Buzzard, Bedfordshire, and extended its geological range to Lower Albian–Cenomanian. It is noteworthy that the ecological conditions at Leighton Buzzard during the Lower Albian were different from any others at that time in the United Kingdom, with the possible exception of the Melton Carstone, in Yorkshire. They were, however, very similar to those of part of the Tournai district in Belgium.

The genus *Boubeithyris* is represented in the British Cenomanian by *B. diploplicata* sp. nov., a species formerly referred to '*Terebratula biplicata*', *sensu* J. Sowerby (1815) and J. de C. Sowerby (1825).

Boubeithyris diploplicata sp. nov.
Fig. 17; Pl. 7, figs 1–3; Pl. 8, figs 4–24

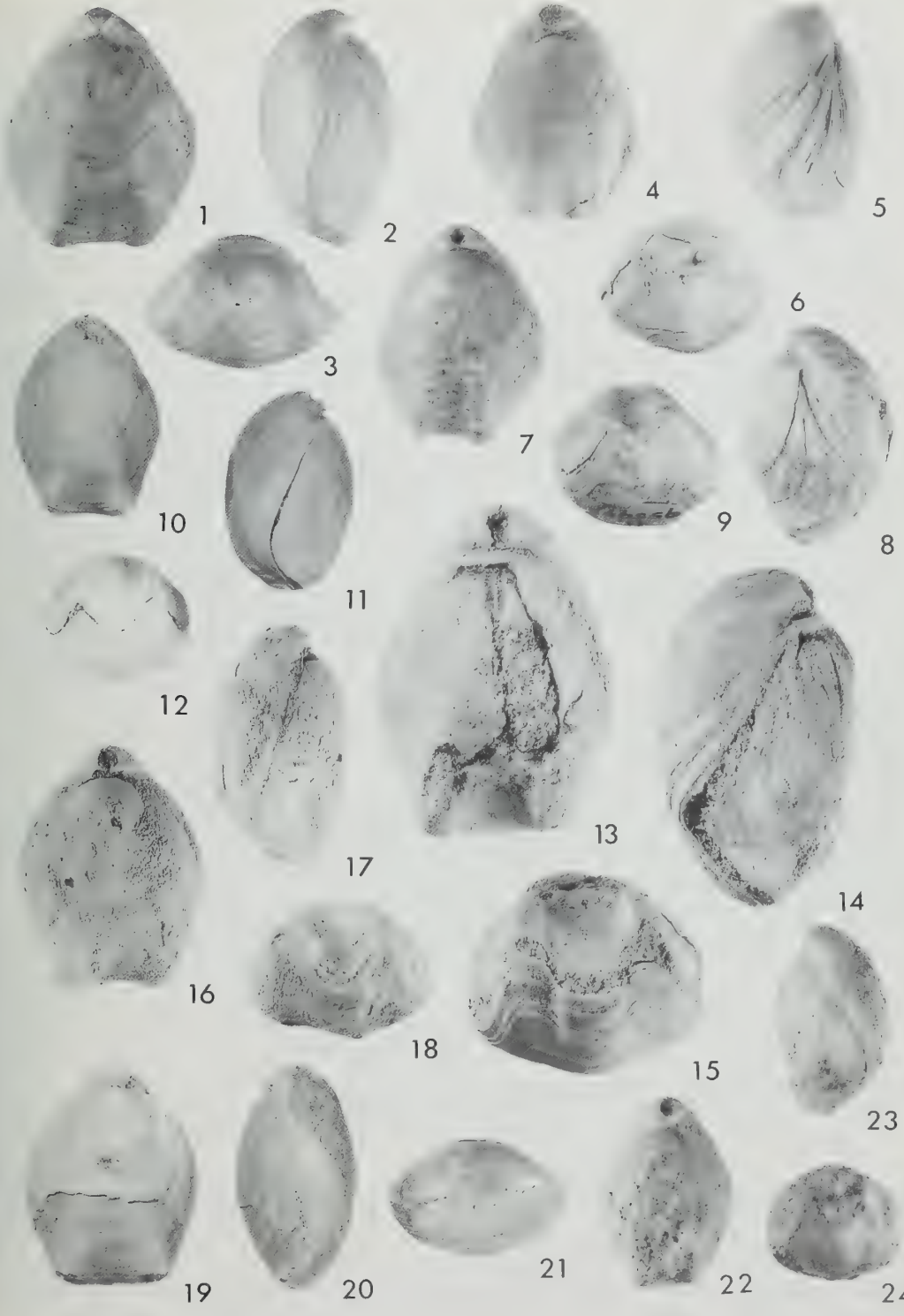
1815 *Terebratula biplicata* J. Sowerby: 201; pl. 90, figs 2–5 (*non* fig. 1, = *Moutonithyris dutempleana* (d'Orbigny)).
1852 *Terebratula biplicata* Brocchi; Davidson: pl. 6, figs 34–39.
1867 *Terebratula biplicata* Sow.; Schloenbach: pl. 21, figs 1–3.
1871 *Terebratula biplicata* Sow.; Quenstedt: pl. 48, figs 61–62.
1903 *Terebratula biplicata* Sow.; Jukes-Browne & Hill: 123, 129.
1969 *Terebratula dutemplei* d'Orbigny: Panow: 583; pl. CXI, figs 1–3.

DIAGNOSIS. Elongate-oval, to pentagonal, to subquadrate in outline. Beak short, suberect.

PLATE 8

Figs 1–3 *Tropeothyris vectis* sp. nov. Lower Cenomanian, Mont Ste Catharine, Rouen, France. B6156, × 1½.

Figs 4–24 *Boubeithyris diploplicata* sp. nov. Figs 4–6, Upper Greensand, Compton Bay, Isle of Wight. B25281, × 1½. Figs 7–9, Upper Greensand, Warminster, Wiltshire. **Holotype** B95597, × 1½. Figs 10–12, Lower Cenomanian, Vimoutiers (Orne), Normandy. B6289, × 1½. Figs 13–15, Upper Greensand, Rocken End, Isle of Wight. BB69002, × 1½. Figs 16–18, Cenomanian, Warminster, Wiltshire. BB76462, × 1½. Figs 19–21, Glauconitic Marl, Eastbourne, Sussex. BB82349, × 1½. Figs 22–24, Glauconitic Marl, Fécamp, Normandy. B35066, × 1½.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Foramen large, circular, mesothyridid; attrite to marginate. Anterior commissure strongly biplicate to sulciplicate.

Cardinal process well developed, hinge-plates thin, ventrally concave, transverse band moderately highly arched.

NAME. 'Doubly folded'.

DESCRIPTION. Although the species is variable it is distinguished by its very acute anterior paraplication and strong biconvexity. The foramen is large and circular, and the beak-ridges well defined. The ventral umbo is short and massive and the interarea poorly developed and obscured by the dorsal umbo. Growth-lines developed throughout growth, but are particularly evident at the shell margins.

HOLOTYPE. B95597; from the Lower Cenomanian, Upper Greensand; Warminster, Wilts. Length 28·5 mm; width 21·5 mm; thickness 20·6 mm (Pl. 8, figs 7–9).

PARATYPES. B95590–602, Warminster; BB5578–89, Maiden Bradley; B6221, Undercliff, Isle of Wight; BB6900, Rocken End, Isle of Wight; B35063, Cap de la Hève, near Le Havre, Normandy; B85265, Auberville, Normandy; B6124, Vimoutiers (Orne), France.

REMARKS. This species was often recorded as '*Terebratula biplicata* Sowerby', but that specific name had already been used for a Jurassic species by Brocchi (1814). Davidson (1852) followed Sowerby in identifying the acutely biplicate species from beds of Lower Cenomanian age in the Warminster district as *T. biplicata* Sowerby. It was thought that the species was confined to localities in Devon, Dorset and Wiltshire but, because of a better understanding of its wide variation in size and degree of convexity, it has since been recognized in the more sandy facies of the Normandy Cenomanian beds. In Britain, the distribution has been extended to the Isle of Wight, where it occurs in the Glauconitic Marl and from the same horizon in basal Cenomanian at Cow Gap, Eastbourne. A splendid series of specimens from the Eastbourne area, showing a wide variation in size, has been kindly lent me by Mr Simon Hurt. In this area the species was formerly represented only by a single specimen in the C. W. Wright collection, but now Pl. 8, figs 19–21 illustrates a further example.

Other localities include Rye Hill Farm and Deverill Hill, near Warminster, and Chute Farm, Wiltshire; a good series of specimens are in the collections of the British Geological Survey, GSM 109902–14, 109924–30, 110036–52 and 111015–35.

The specimens figured by Schloenbach (1867: pl. 21, figs 1–3) came from the Unterer Pläner of north Germany. The specimen figured by Panow (1968: pl. CXI, fig. 1a–c) came from the Cenomanian of the Krakow district, Poland; it was part of a collection described in 1930 but not published until revised by Biernat & Popiel-Barczyk (1969).

All the above specimens are assigned to *Boubeithyris* on the strength of serial sections made from B82750 (Fig. 17). They are similar to the sections of Cox & Middlemiss (1978: 420) and of Cox (née Pinder) (1967, unpublished Ph.D. thesis, University of London).

Subfamily **RECTITHYRIDINAE** Muir-Wood, 1965

Genus ***RECTITHYRIS*** Sahni, 1929

TYPE SPECIES. *Terebratula depressa* Valenciennes, *in* Lamarck, 1819.

Rectithyris wrightorum sp. nov.
Pl. 6, figs 10–12

DIAGNOSIS. Oval, biconvex *Rectithyris*. Umbo short, foramen large, circular; symphytium not exposed. Rectimarginate.

NAME. For Messrs C. W. & E. V. Wright.

DESCRIPTION. The short, massive umbo is truncated by a large circular foramen. Beak-ridges are lacking and the interarea is poorly defined. Growth-lines are numerous but indistinct,

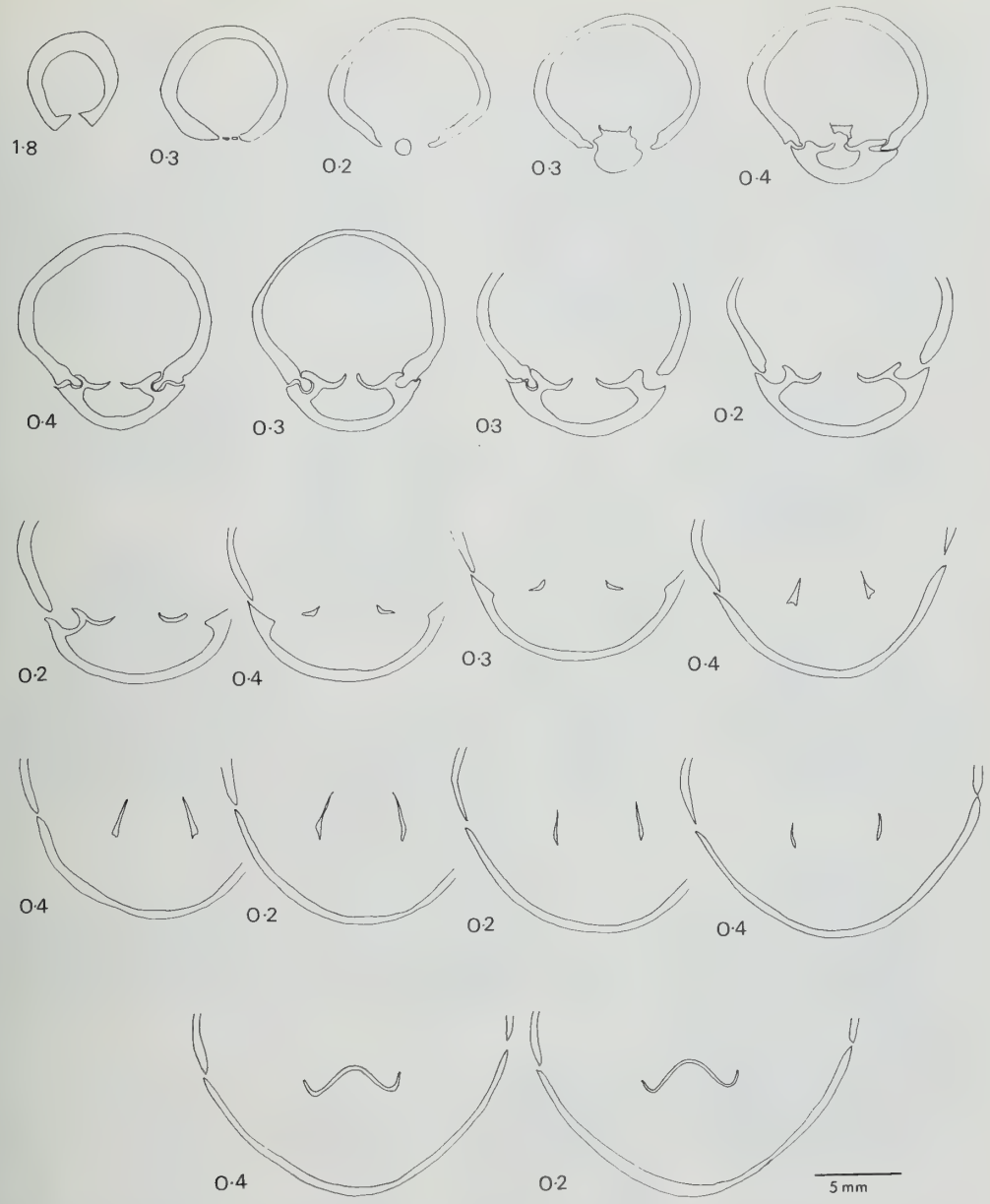


Fig. 17 *Boubeithyris diploplicata* sp. nov. Nineteen transverse serial sections through B82750, from the Upper Greensand of Beuzeville, near Le Havre, Normandy.

becoming clearer towards the margins. The shell is inflated in the dorsal umbo but remains biconvex in lateral profile.

Holotype. C. W. & E. V. Wright Collection, BB82175; from the Lower Cenomanian, 'Grizzle'; White Hart sand pit, Wilmington, south Devon. Length 45·3 mm; width 38·9 mm; thickness 18·9 mm.

PARATYPE. BB82215, collected by Dr W. J. Kennedy from the same locality and horizon as the holotype. Length 45·3 mm; width 38·9 mm; thickness 18·9 mm.

REMARKS. *Rectithyris wrightorum* is an extremely rare species in the Lower Cenomanian of Wilmington, but is probably the ecological equivalent of the type species *R. depressa*, described from the Essen Greensand. The new species differs in its short, massive umbo, whereas the type species, like its equivalent *Terebratula nerviensis* d'Archiac in the Belgian Tourtia, is characterized by its slender, produced umbo and well exposed symphytium. Otherwise the two species have a similar oval outline and exhibit approximately the same degree of biconvexity.

In many ways, a closer morphological comparison is with *Terebratula shenleyensis* Walker, 1903, from the Lower Albian of Leighton Buzzard, Bedfordshire and redescribed with its varieties by Dr M. Cox (1967, Ph.D. thesis), differing from *T. wrightorum* sp. nov. in its oval outline and less acutely inflated brachial valve.

Internal structures remain unknown through a lack of suitable material for sectioning.

Genus *TROPEOTHYRIS* Smirnova, 1972

TYPE SPECIES. *Tropeothyris kugusemi* Smirnova.

Tropeothyris vectis sp. nov.

Fig. 18; Pl. 8, figs 1–3; Pl. 9, figs 1–6, 10–15

DIAGNOSIS. Pentagonal to broadly oval in outline. Umbo short, massive; foramen large, circular. Beak suberect, beak-ridges mesothyridid. Biplication poorly to moderately developed.

NAME. Vectis; ancient name for the Isle of Wight.

DESCRIPTION. The lateral profile is ventri-biconvex, the brachial valve being only gently curved. A shallow sulcus starts at about mid-length of the adult dorsal valve and deepens and broadens anteriorly; it is bordered by faint carinae. Individuals with their maximum width just anterior to the middle of the shell tend to have a stronger biplication at the commissure. Faint growth-lines occur between two or more well-marked growth halts at about half and two-thirds of the adult shell length.

INTERNAL CHARACTERS. Transverse serial sections (Fig. 18) display a pedicle collar and a wide symphytium. A low, flat cardinal process can be seen in section 7, just after the first appearance of the dorsal umbo. Short, ventrally concave hinge-plates elongate slightly and become virgate. Thickened crural bases give rise to long, slender, inwardly curving and rapidly diminishing crural processes. A low arched transverse band terminates the loop approximately 8·5 mm from the ventral umbo.

HOLOTYPE. E. F. Owen Collection, BB82185; from the Glauconitic Marl; Gore Cliff, Isle of Wight. Length 30·2 mm; width 22·4 mm; thickness 16·6 mm.

PARATYPES. B6221 from Culver Cliff, Isle of Wight; B24944 from the Glauconitic Marl of Folkestone Warren, Kent.

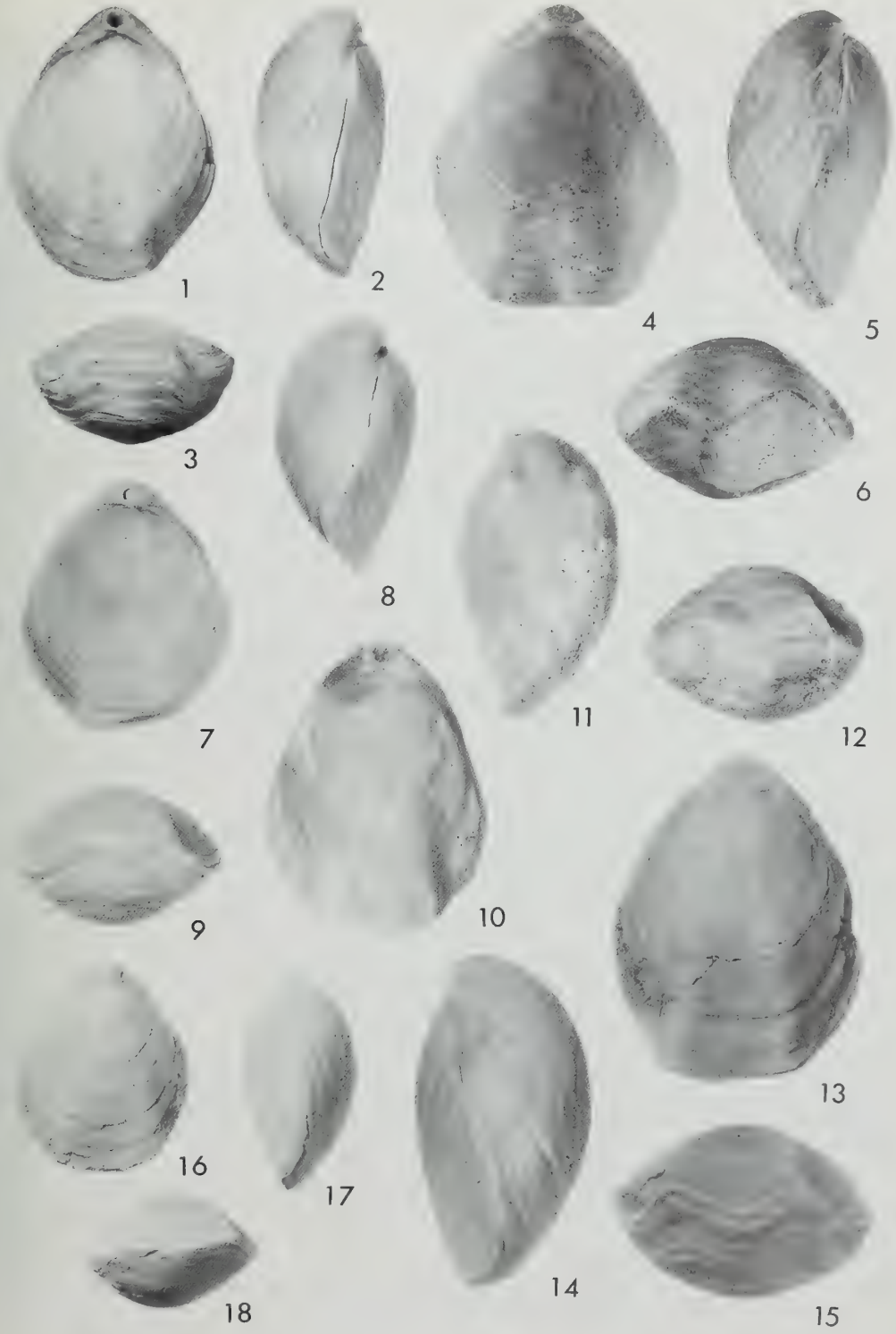
PLATE 9

Figs 1–3 *Terebratula carteri* Davidson (? = *Tropeothyris*). Lower Cenomanian, Folkestone, Kent. Davidson Collection, B6126, × 1½.

Figs 4–6, 10–15 *Tropeothyris vectis* sp. nov. Figs 4–6, Upper Greensand, Rocken End, Isle of Wight. BB82331, × 1½. Figs 10–12, Glauconitic Marl, Gore Cliff, Isle of Wight. **Holotype** BB82185, × 1½. Figs 13–15, Glauconitic Marl, Folkestone Warren. B24944, × 1½.

Figs 16–18 *Tropeothyris* sp. Cenomanian, Loudon Road Pit 19, near Louth, Lincolnshire. BB55022, × 1½.

Figs 7–9 Undescribed species. Lower Cenomanian, Julianka, Annopol, Poland. BB82181, × 1½.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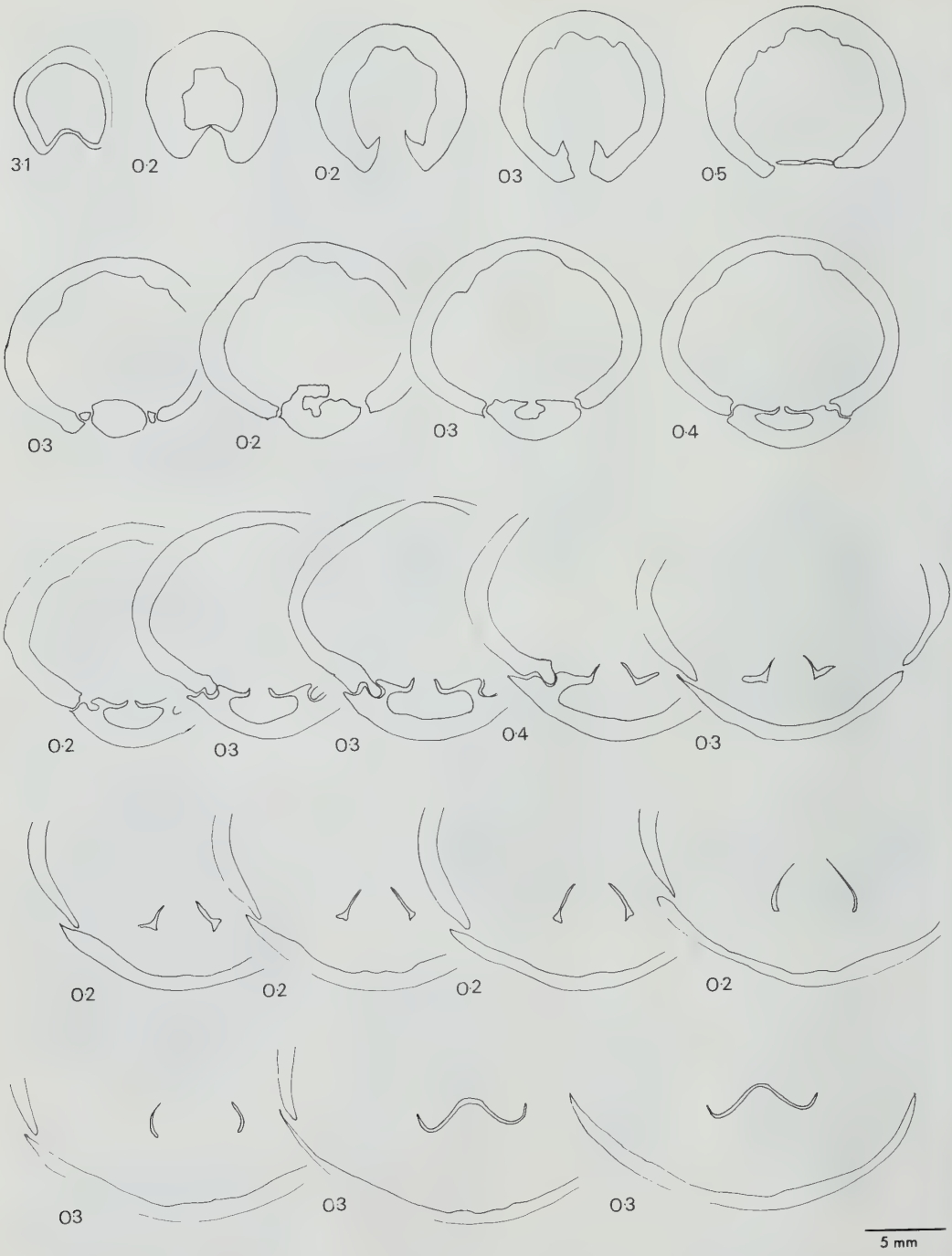


Fig. 18 *Tropeothyris vectis* sp. nov. Twenty-one transverse serial sections through BB82331, from the Glauconitic Marl, Rocken End, Isle of Wight.

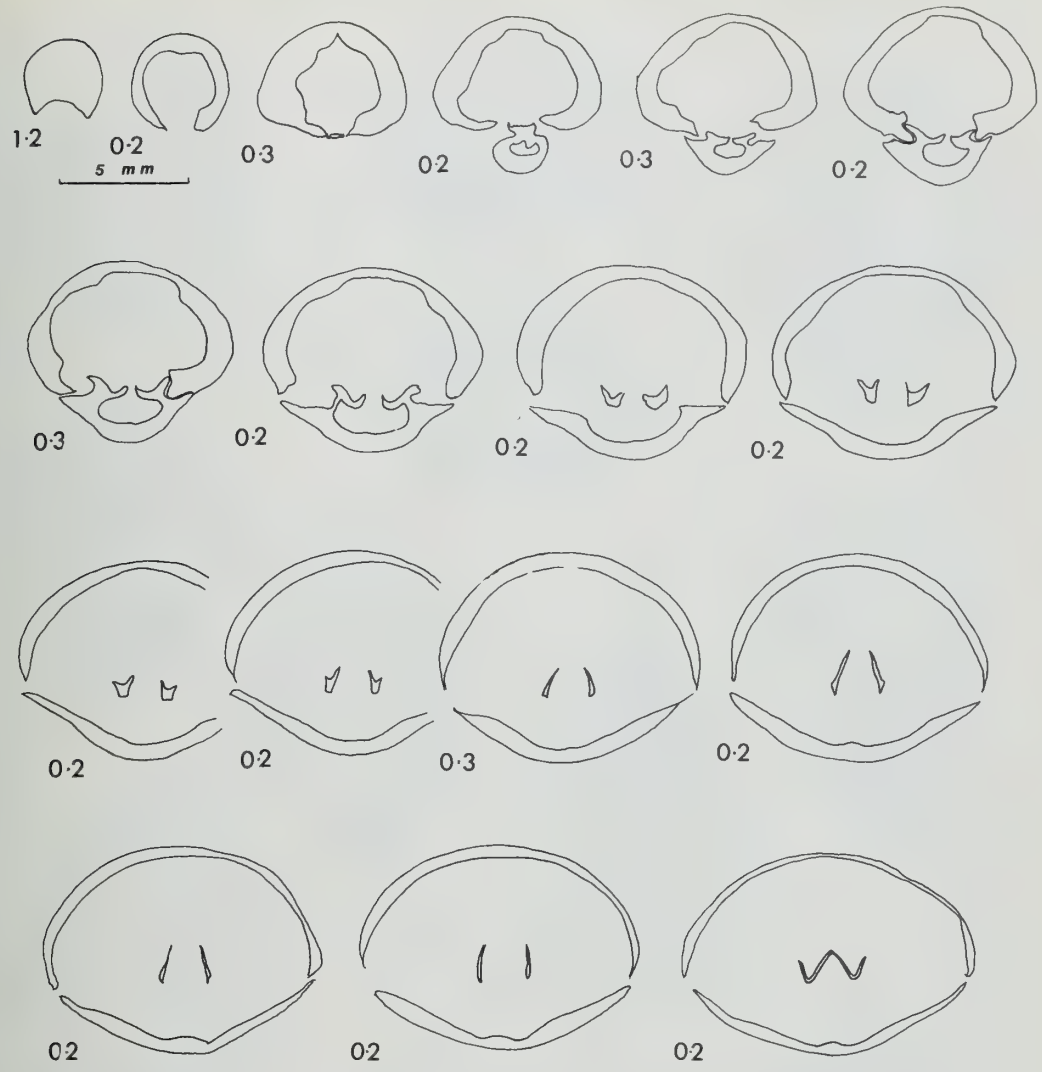


Fig. 19 *Tropeothyris* sp. Seventeen transverse serial sections through a specimen from the Lower Cenomanian of Julianka, Annopol, Poland.

REMARKS. Specimens have also been collected from Eastbourne in beds of early Cenomanian age. *Terebratula carteri* Davidson (1852: 72; pl. 7, fig. 3) may belong to this genus but it differs from the species described here in its uniplicate anterior commissure and slightly more produced umbo. An undescribed specimen which might belong with *T. vectis* was collected from Pit 19, Loudon Road, Louth, Lincolnshire (Pl. 9, figs 16–18). It is more regularly oval in outline than the typical form and has a less acutely developed anterior plication. It appears to be closely related to another undescribed species from the Lower Cenomanian of Annopol on the Vistula, Poland (Pl. 9, figs 7–9). Serial sections of a specimen from the Phosphate Mine, Julianka, Annopol, Poland (Fig. 19) can be compared to sections through a specimen of *Tropeothyris vectis* (Fig. 18) and to sections through a specimen from Loudon Road Pit, Louth, Lincolnshire (Fig. 20). Each series has much in common, but more research is necessary before their relationships can be elucidated.

DIMENSIONS of some BM(NH) specimens. Measurements in mm.

Number	length	width	thickness
Glauconitic Marl; Rocken End, I. o. W. C. W. & E. V. Wright Colln:			
BB69001	22·6	19·6	14·9
BB69004	26·3	21·1	14·5
BB69005	22·0	18·8	11·8
BB69006	24·6	17·8	13·0
BB69007	17·4	15·2	12·8
BB69009	25·3	19·5	13·8
Glauconitic Marl; Rocken End, I. o. W. W. J. Kennedy Colln:			
BB82122	27·0	20·8	16·1
BB82123	24·2	22·0	13·1
BB82124	22·0	17·1	12·3
BB82125	21·4	18·1	9·6

Number	length	width	thickness
Mantelli Zone; Eastbourne. W. J. Kennedy Colln:			
BB82303	25·9	21·9	14·3
BB82304	27·3	21·4	16·1
BB82111	31·2	21·4	15·9
BB82112	33·8	26·8	16·4
BB82113	31·7	25·1	15·0
BB82114	29·0	22·8	13·6
BB82115	24·1	19·5	9·7
Glauconitic Marl; Ventnor, I. o. W. F. Stinton Colln:			
BB9298	29·2	25·7	12·8
BB9299	26·0	20·7	12·0
BB9300	23·8	18·5	13·6
BB9301	24·4	19·1	13·5

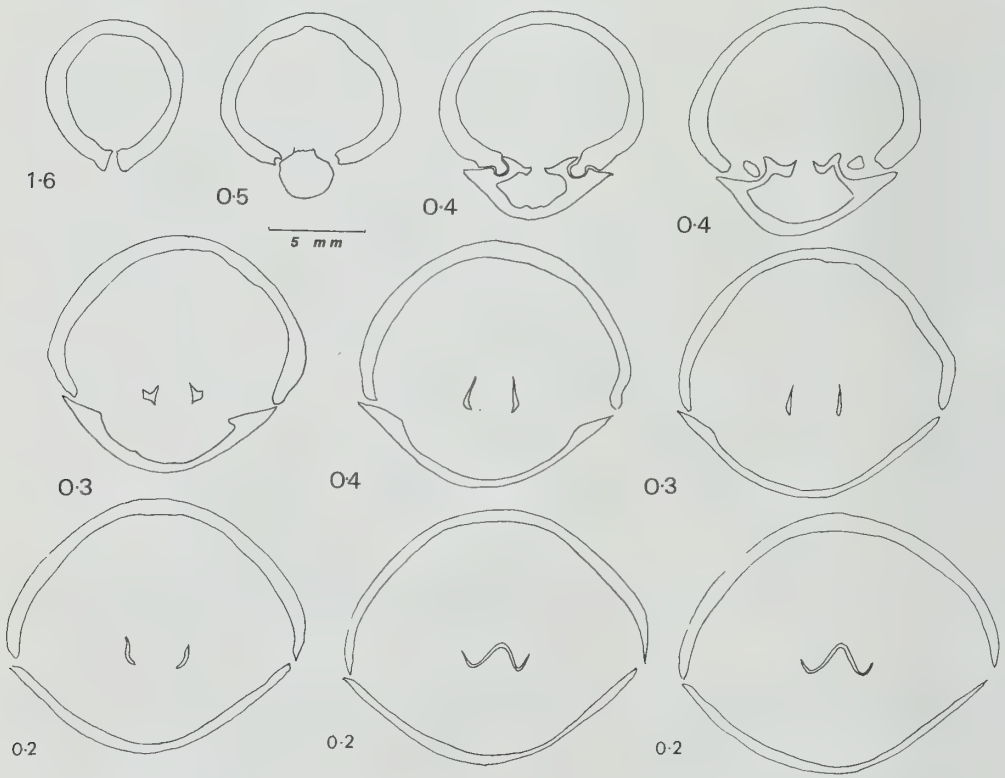
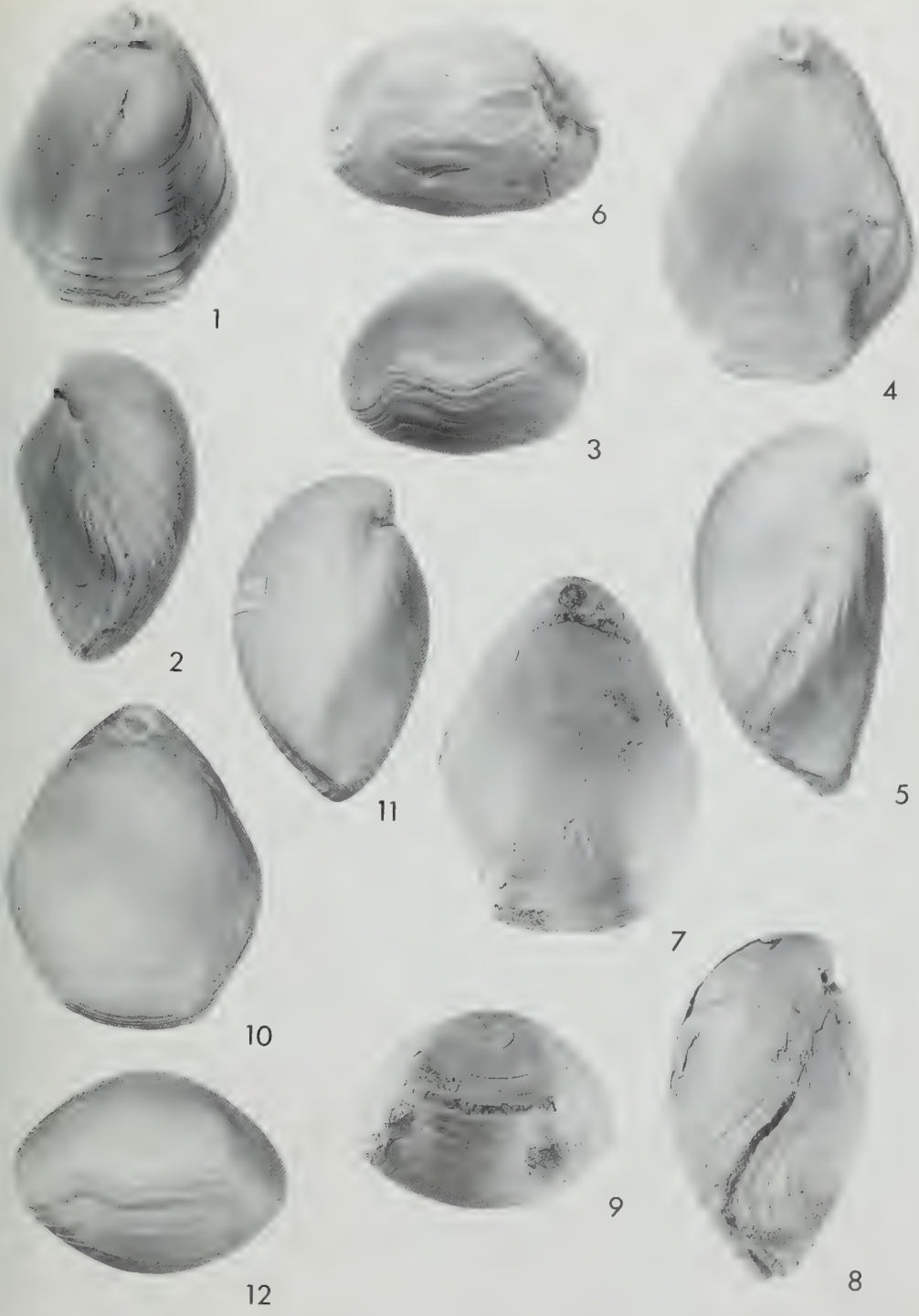


Fig. 20 *Tropeothyris* sp. Ten transverse serial sections through a specimen from the Loudon Road Pit, Louth, Lincolnshire, of Middle Cenomanian age.

PLATE 10

Figs 1–12 *Moutonithyris dutempleana* (d'Orbigny). Figs 1–3, Bed B, Red Rock, Hunstanton Cliff, Norfolk. BB82345, × 1½. Figs 4–12, Cenomanian, Cambridge Greensand, Cambridge. Figs 4–6, BB21188, × 1½. Figs 7–9, B25177, × 1½. Figs 10–12, variant, B25161, × 1½.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Genus *MOUTONITHYRIS* Middlemiss, 1976

TYPE SPECIES. *Terebratula moutoniana* d'Orbigny, 1849

Moutonithyris dutempleana (d'Orbigny)
Fig. 21; Pl. 10; Pl. 11, figs 4–6; Pl. 18, figs 23–24

1815 *Terebratula biplicata* J. Sowerby: 201; pl. 90, fig. 1 (*non* figs 2–5; see p. 112).
1823 *Terebratula biplicata* Sow.; J. de C. Sowerby: 53; pl. 437.
1849 *Terebratula Dutempliana* d'Orbigny: 93; pl. 511, figs 1, 2, 3, 6, 7 (*non* figs 4, 5).
1855 *Terebratula biplicata* Brocchi; Davidson: 55; pl. 6, figs 1–30.
1960 *Terebratula dutempleana* d'Orb.; Pauca & Patrulius: 88; pl. 2, fig. 10.
1975 *Terebratula dutempleana* d'Orbigny; Middlemiss (*in* Dieni, Middlemiss & Owen): 186; pl. 33, fig. 2; text-fig. 9.
1976 '*Terebratula*' *dutempleana* d'Orbigny; Gaspard: pls 1–5.

LECTOTYPE. B61531; from the Cambridge Greensand, Castle Hill, Cambridge; figured by J. Sowerby, 1815: pl. 90, fig. 1. Selected Middlemiss (1975).

REMARKS. Until this species was revised by Middlemiss (1975), it had been broadly interpreted, and had become confused with interpretations of Brocchi's Jurassic species *T. biplicata* Brocchi.

There is, unfortunately, some uncertainty over the exact stratigraphical horizon of the lectotype, since the term 'Cambridge Greensand' includes the Upper Albian to Middle Cenomanian. The adopted concept of *M. dutempleana* (d'Orbigny), based on the lectotype, includes the commonly-occurring terebratulid species with its greatest shell width at just over half its total length and with a marked plication of the anterior commissure. The species is found as both derived and indigenous fossils within the Cambridge Greensand in the Cambridge area, and as a common fossil in the Red Rock of Hunstanton Cliff, north Norfolk. The beds within this part of the Hunstanton section fall within the Middle to Upper Albian and have been divided into three distinct lithological units, A, B and C, with Bed C at the bottom resting on the Carstone. According to Dr H. G. Owen (personal communication), who has worked on ammonite species within this series, Bed C is in the *Anahoplites intermedius* Subzone of the Middle Albian, Bed B within the upper part of the *cristatum* Subzone, and Bed A has a lighter band representing the *Hysteroceras varicosum* Subzone at the base and a darker band within the *?Callihoplites auritus* Subzone at the top. Both Beds A and B are of Upper Albian age.

The commonest variant found in Beds A and B at Hunstanton and in the Cambridge Greensand is represented by two specimens figured here, from the Upper Albian of Hunstanton (Pl. 10, figs 1–3), and from the Cambridge Greensand (Pl. 10, figs 4–6). Variation within the species affects the oval outline and degree of biplication of the anterior commissure (see Pl. 10, figs 7–9 & 10–12).

Occurring with *M. dutempleana* in both the Cambridge and Hunstanton beds is *Terebratula obtusa* J. de C. Sowerby (1825). This species was included in Davidson's (1855) synonymy of *M. dutempleana* (then described as *Terebratula biplicata*), but in fact the two differ considerably. *T. obtusa* maintains a consistently pentangulate outline, flatter dorsal umbo and a uniplicate to incipiently biplicate anterior commissure; its growth-lines appears to occur more frequently, encouraging some workers to assign it to *Ornatothyris*. The constant association of these two species extends beyond Britain, and can be recognized in assemblages of Terebratulidae including forms thought to be very closely related to *Moutonithyris dutempleana* from beds of Cenomanian age at Drap, near Nice, southern France. The two species are now known to be congeneric and it has been suggested that this association might demonstrate sexual dimorphism. Serial sections of specimens from the Cambridge Greensand, similar specimens from the Upper Albian beds of the Red Rock at Hunstanton, and specimens of *Moutonithyris dutempleana* from Hunstanton (Fig. 21) and the type locality at Cambridge all resemble each other. Examples of *Moutonithyris obtusa* (Pl. 11, figs 7–9; Pl. 12, figs 4–6) from the Cambridge Greensand can be compared with *M. dutempleana* (Pl. 11, figs 4–6) from Bed A, Red Rock, Hunstanton. *M. dutempleana* occurs uncommonly in the Upper Gault, Price's (1877) Bed X, at Folkestone, Kent (Pl. 18, figs 23–24).

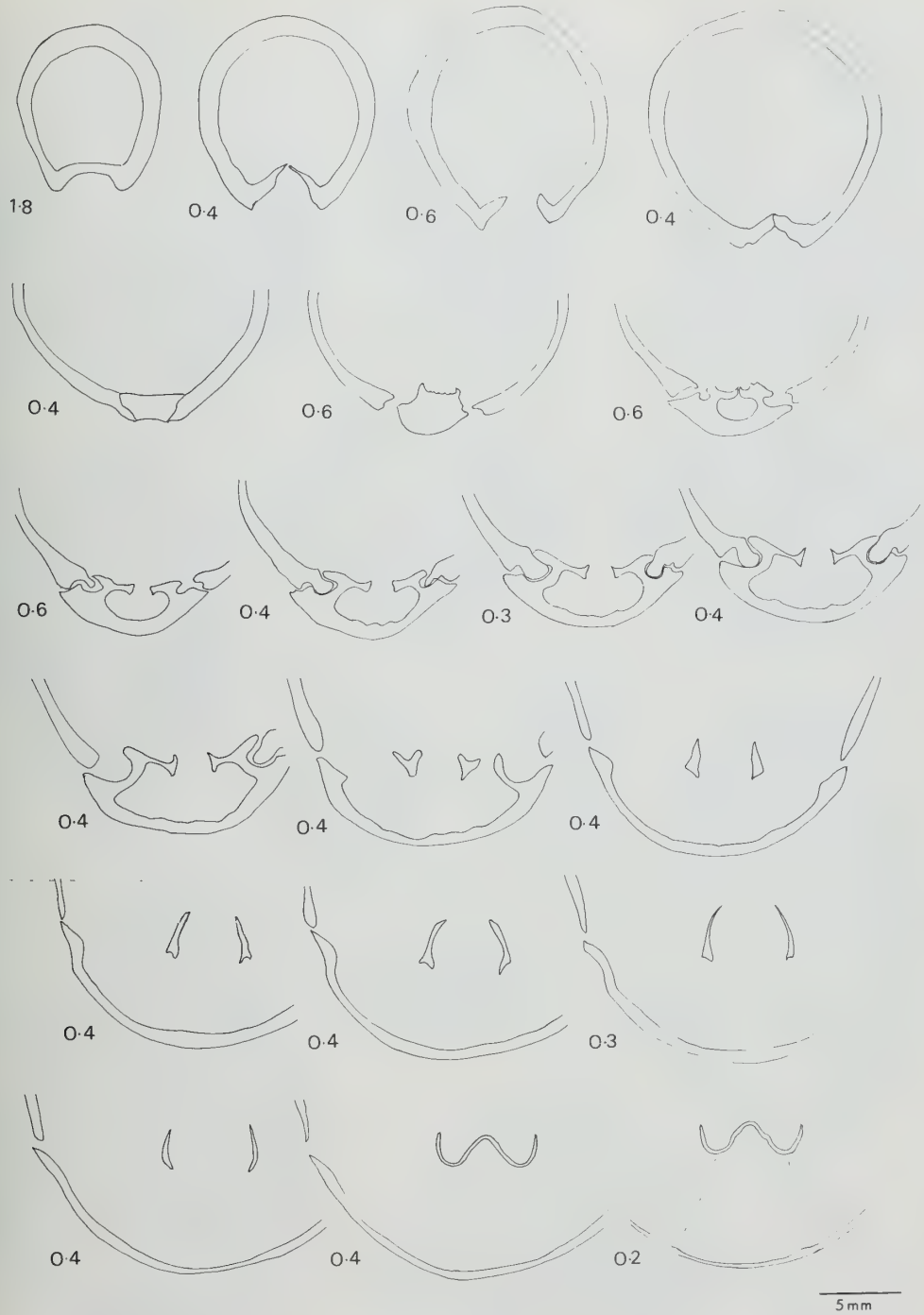

Fig. 21 *Moutonithyris dutempleana* (d'Orbigny). Twenty transverse serial sections through BB82333 (Le Strange colln), from Bed A, Red Rock, Hunstanton Cliff, Norfolk.

Frebold (1935), in describing a brachiopod fauna from the marine Upper Aptian of Koldewey Island, north-east Greenland, included a specimen he called *Terebratula biplicata* (1935: pl. 8, figs 1–3), the general form of which is very close to *Moutonithyris dutempleana* described here from the Cambridge Greensand and Red Rock of Hunstanton. Frebold figured an associated crushed specimen with capillate ornament (1935: pl. 8, fig. 4), which is very similar to *Capillithyris capillata* (d'Archiac), the species associated with *Moutonithyris* species at Hunstanton.

Cooper (1983), in his major study of terebratulacean loops, described a new genus and species commonly occurring in the Upper Albian Red Rock of Hunstanton, Norfolk, which had been called '*Terebratula*' *dutempleana* d'Orbigny. This species was assigned to *Moutonithyris* by Middlemiss (1976: 63) when he erected the genus. As a result of careful hand dissection of the brachidia and cardinalia, Cooper was able to expose certain internal characteristics in a specimen of that species which are not seen in serial sections published by Gaspard (1976) and Middlemiss (*in* Dieni, Middlemiss & Owen 1975). Cooper displayed the fairly wide concave hinge-plates attached to the ventral part of the crural bases, and the acutely high folded and broad transverse band at the front of the brachial loop. The description of these characters conflicts with that of *Moutonithyris* given by Middlemiss (1976) in which he stressed the low arching of the transverse band and the cuneate, keeled hinge-plates. However, transverse serial sections of *Mountonithyris dutempleana* (d'Orbigny) and *M. anglia* sp. nov. (p. 126) from the Red Rock of Hunstanton (Figs 21, 22) do not support Cooper's description of the ventral attachment of the outer hinge-plates but do agree in the presence of a short, broad loop, slightly expanded anteriorly and with an acute transverse band, characters shown also in transverse serial sections by Gaspard (1976) of another specimen from the Red Rock of Hunstanton.

Cooper described as new *Biplicatoria feruginea*, the type species of his new genus, and *B. hunstantonensis* from the top bed (Bed 3 = Bed A) of the Upper Albian, Red Rock. I contend that *Moutonithyris dutempleana* (d'Orbigny) occurs predominantly in Bed 3 (Bed A) and that *M. anglia* sp. nov. is restricted to Bed 1 (Bed C) at the base of the Red Rock.

Thus while acknowledging Dr Cooper's work I do not accept that *M. dutempleana* should be transferred to *Biplicatoria*, nor do I believe that the specimens figured by him (Cooper 1983: pl. 20, figs 21–27; pl. 21, figs 1–6) as *Biplicatoria hunstantonensis* and *B. feruginea* are other than variants of *Moutonithyris dutempleana* (d'Orbigny), although this requires confirmation.

MATERIAL. Numerous specimens of *Moutonithyris dutempleana* (d'Orbigny) are housed in the British Museum (Natural History), British Geological Survey, and the Sedgwick Museum, Cambridge. Specimens of *M. obtusa* also occur in the same institutions but are less numerous. Six specimens from the Upper Albian, Red Rock of South Cave, Humberside are in the collections of the British Museum (Natural History), nos 68962–7, and show a very close resemblance to the type specimen from the Cambridge Greensand.

DIMENSIONS. The following measurements (in mm) are from BM(NH) specimens from Beds A and B in the Red Rock, Hunstanton, Norfolk, collected by Mr H. Le Strange.

PLATE 11

Figs 1–3 *Ornatothyris sabinensis* (Parent). Tourtia, Tournai, Belgium. BB82188, × $1\frac{1}{2}$.
Figs 4–6 *Moutonithyris dutempleana* (d'Orbigny). Bed A, Red Rock, Hunstanton Cliff, Norfolk. BB82180, × $1\frac{1}{2}$.
Figs 7–9 *Moutonithyris obtusa* (J. de C. Sowerby). Cambridge Greensand, Cambridge. BB6006, × 1.
Figs 10–12 *Concinnithyris davidsoni* (Rollier). Tourtia, St Aybert, Belgium. Int. Sci. roy. Belg. I.G. 8261, × $1\frac{1}{2}$.

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Number	length	width	thickness	Number	length	width	thickness
BB82350	37·2	30·8	21·6	BB82355	34·0	26·3	19·1
BB82351	34·0	27·9	20·2	BB82356	31·1	25·5	18·9
BB82352	34·5	25·0	19·1	BB82357	30·2	23·6	18·0
BB82353	30·8	25·1	19·9	BB82358	27·9	23·4	17·1
BB82354	31·1	25·5	19·0	BB82359	29·3	23·4	17·2

Moutonithyris anglia sp. nov.
Fig. 22; Pl. 6, figs 22–24

DIAGNOSIS. Consistently oval in outline. Maximum width at half valve length. Strongly ventribiconvex. Uniplicate to incipiently biplicate. Umbo truncated by large circular foramen; beak suberect.

NAME. 'England'.

DESCRIPTION. Because of their similarity, this species has, until now, been compared with *M. dutempleana*. *Moutonithyris anglia*, however, has a consistent oval outline and a very marked

Fig. 22 *Moutonithyris anglia* sp. nov. Twenty-one transverse sections through B2221 from Bed C, Red Chalk, Hunstanton Cliff, Norfolk.

even biconvexity. The anterior commissure is uniplicate to faintly biplicate, never showing the acute biplication of *M. dutempleana*. The umbo is massive and dominated by the large circular foramen with permesothyridid beak-ridges. *M. anglia* does not have a labiate foramen like that of *M. dutempleana*, and the symphytium is never exposed.

INTERNAL CHARACTERS. Transverse serial sections (Fig. 22) show that this species, like all species assigned here to *Moutonithyris*, has the same low, poorly developed cardinal process, and the short, ventrally concave initial hinge-plates which lengthen, becoming almost horizontal and keeled before being deflected dorsally. The terminal ends of the hinge-plates thicken, giving rise to V-shaped bases which change anteriorly into the descending branches of the brachial loop. This elongates ventrally, giving off inwardly curving crural processes, which diminish anteriorly. The transverse band is a low-arched, comparatively broad W-shaped ribbon. This structure is quite commonly associated with a feature called the 'sub-loop skirt' by Cox & Middlemiss (1978) and probably resulted from coalescence of spicules within the mantle in the living specimen. Oddly, this character has been observed in specimens of *M. dutempleana* and *M. obtusa* from Beds A and B and in specimens from the Cambridge Greensand, but does not seem to occur in sectioned specimens from Bed C described here as *M. anglia*.

HOLOTYPE. Collected by H. Le Strange, BB82262; from Bed C of the Red Rock, Hunstanton cliffs, Norfolk. Length 40·1 mm; width 30·2 mm; thickness 24·2 mm. Pl. 6, figs 22–24.

PARATYPES. Ten specimens from the type locality and horizon, BB82263–72. Dimensions given below.

REMARKS. This is the only *Moutonithyris* species occurring in Bed C of the Red Rock. It can be distinguished from other species of *Moutonithyris* by its consistent elongate-oval outline with its maximum width at half the valve length, large circular foramen, and gently uniplicate to faintly biplicate anterior commissure.

DIMENSIONS of paratypes. Measurements in mm.

Number	length	width	thickness	Number	length	width	thickness
BB82263	29·3	20·9	19·1	BB82268	31·2	24·5	16·5
BB82264	36·6	27·6	20·4	BB82269	32·4	25·6	17·4
BB82265	33·1	26·1	20·3	BB82270	30·8	25·1	18·2
BB82266	30·2	23·4	18·4	BB82271	27·9	23·0	17·2
BB82267	31·1	22·4	17·1	BB82272	29·9	23·2	15·9

Subfamily **NERTHEBROCHINAE** Cooper, 1983

Genus ***HARMATOSIA*** Cooper, 1983

Harmatosia crassa (d'Archiac)

Pl. 6, figs 4–6

1847 *Terebratula tornacensis* var. *crassa* d'Archiac: 318; pl. 18, figs 8a–d.
1983 *Harmatosia crassa* (d'Archiac) Cooper: 196; pl. 19, figs 13–22; pl. 29, figs 8–11; pl. 67, figs 5, 10, 11.

REMARKS. This species was originally described as a variety of *Terebratula tornacensis* by d'Archiac (1847) from the Tourtia of the Tournai district, Belgium. Cooper (1983) chose it as type species of his new genus *Harmatosia* and an example, from the type locality, is illustrated here (Pl. 6, figs 4–6), for comparison with *Sellithyris tornacensis* (d'Archiac) (p. 104; Pl. 6, figs 1–3).

RANGE. Cenomanian.

Family **GIBBITHYRIDIDAE** Muir-Wood, 1965

Subfamily **GIBBITHYRIDINAE** Muir-Wood, 1965

Genus ***CONCINNITHYRIS*** Sahni, 1929

TYPE SPECIES. *Terebratula obesa* J. de C. Sowerby 1823.

EMENDED DIAGNOSIS. Elongate-oval to subcircular in outline. Umbo massive, beak slightly incurved to erect, truncated; foramen small to large, circular, permesothyridid, rarely labiate; beak ridges indistinct. Anterior commissure rectimarginate, to uniplicate, to biplicate.

Cardinal process low, flat, poorly developed. Hinge-plates fairly long, ventrally convex from anterior ends of which crural bases develop. Crural processes high, tapering, inwardly curving. Thin descending branches of brachial loop with low arched transverse band, sometimes with small depression or sulcus posteriorly.

RANGE. Upper Albian to Cenomanian.

REMARKS. In his description of the brachial loop of *Concinnithyris*, Cooper (1983: 183) gave the stratigraphical range as Neocomian to Turonian and included the species *C. albensis* (Leymerie), *C. obesa* (Sowerby), *C. burhamensis* Sahni and *C. rouenensis* Cooper, 1983. Although disagreeing with Cooper's (1983) wider stratigraphical range, I believe the genus may be represented within the basal beds of the Lower Turonian in France.

The interpretation of this genus depends upon the interpretation of the type species, *T. obesa* J. de C. Sowerby. As the holotype is the only representative of this species in the Sowerby Collection, and is from an unrecorded horizon at Norton Bavant, Wiltshire, Sahni (1929) must have based his description of the genus on this and other specimens from different localities which he identified as *T. obesa*. Although he states the range of the type species to be Turonian, he dissected a specimen from Eggardon Hill, Dorset, B24914, which is probably also *T. obesa*. This locality has been reinterpreted by Kennedy (1970) as of *jukesbrownei* assemblage age, at the top of the *Acanthoceras rhotomagense* Zone of the Middle Cenomian. Sahni's age determination was probably based upon data recorded by d'Orbigny (1847) who cited conspecific specimens from the 'Turonien Superieur' of Rouen, and it is indeed a comparatively common fossil within the *A. rhotomagense* Zone in the Craie de Rouen.

Concinnithyris obesa (J. de C. Sowerby)
Fig. 23; Pl. 12, figs 7–12; Pl. 14

1823 *Terebratula obesa* J. de C. Sowerby: 54; pl. 438, fig. 1.
1850 *Terebratula obesa* J. de C. Sowerby; d'Orbigny: 105; pl. 513, figs 1–3 (*non* fig. 4).
1929 *Concinnithyris obesa* (J. de C. Sowerby) Sahni: 12; pl. 1, figs 1–9; pl. 8, figs 1–2.

HOLOTYPE. Sowerby Collection, B49832; from the Lower Chalk; Norton Bavant, Wiltshire. Length 48·9 mm; width 36·0 mm; thickness 34·9 mm.

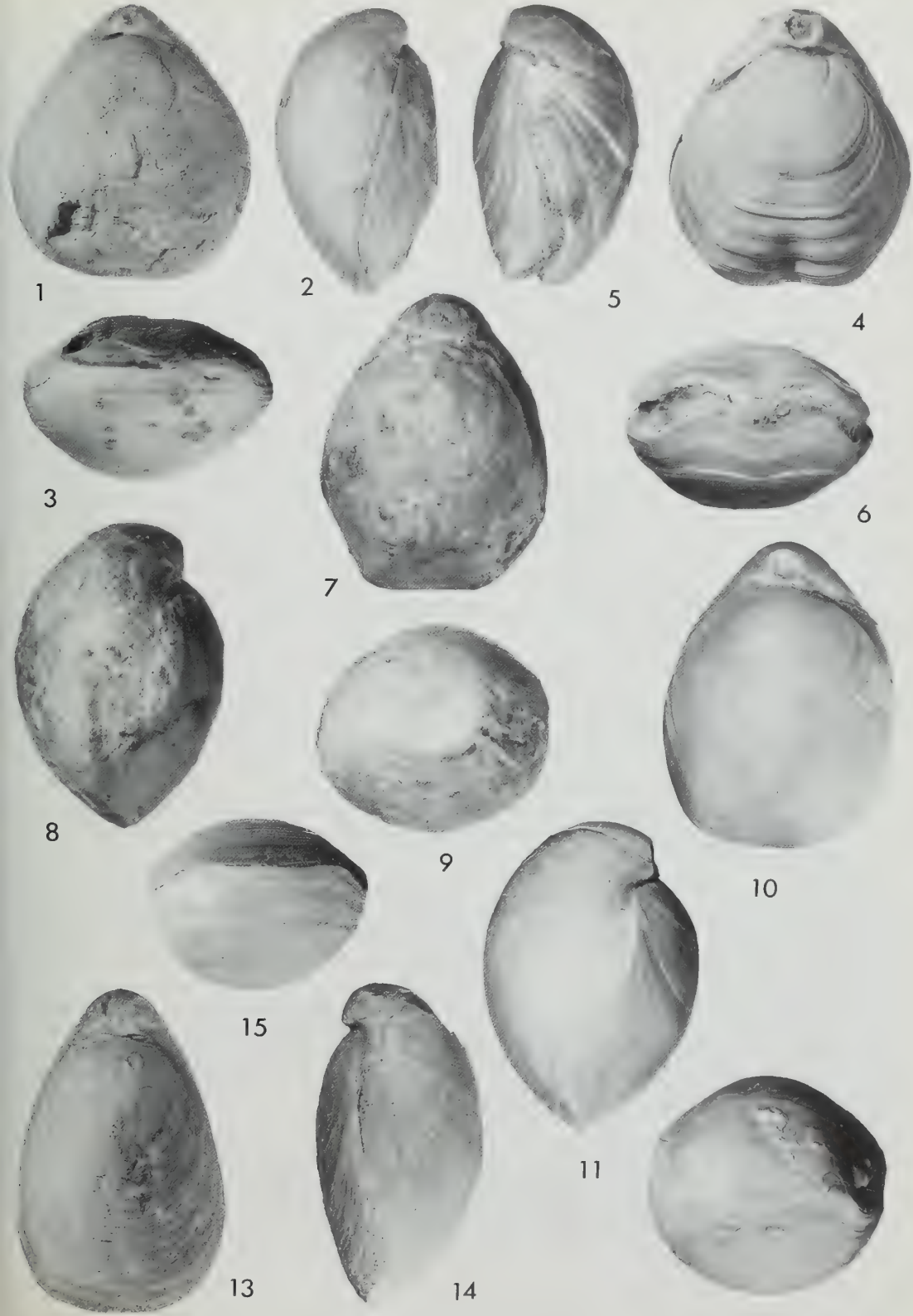
PLATE 12

Figs 1–3 *Ornatothyris latissima* Sahni. Plenus Subzone, South Ferriby, S. Humberside. BB82202, × $1\frac{1}{2}$.

Figs 4–6 *Moutonithyris obtusa* (J. Sowerby). Cambridge Greensand, Cambridge. IGS unregistered specimen, × $1\frac{1}{2}$.

Figs 7–12 *Concinnithyris obesa* (J. Sowerby). Figs 7–9, Cenomanian, Storridge Hill, Chardstock, Devon. BB84905, × $1\frac{1}{2}$. Figs 10–12, Bed C, Cenomanian, Shapwick Farm, near Uplyme, Dorset. BB82172, × $1\frac{1}{2}$.

Figs 13–15 *Ornatothyris* cf. *pentagonalis* Sahni. First *Inoceramus* Bed, Lower Cenomanian, Hunstanton Cliff, Norfolk. BB82302, × $1\frac{1}{2}$.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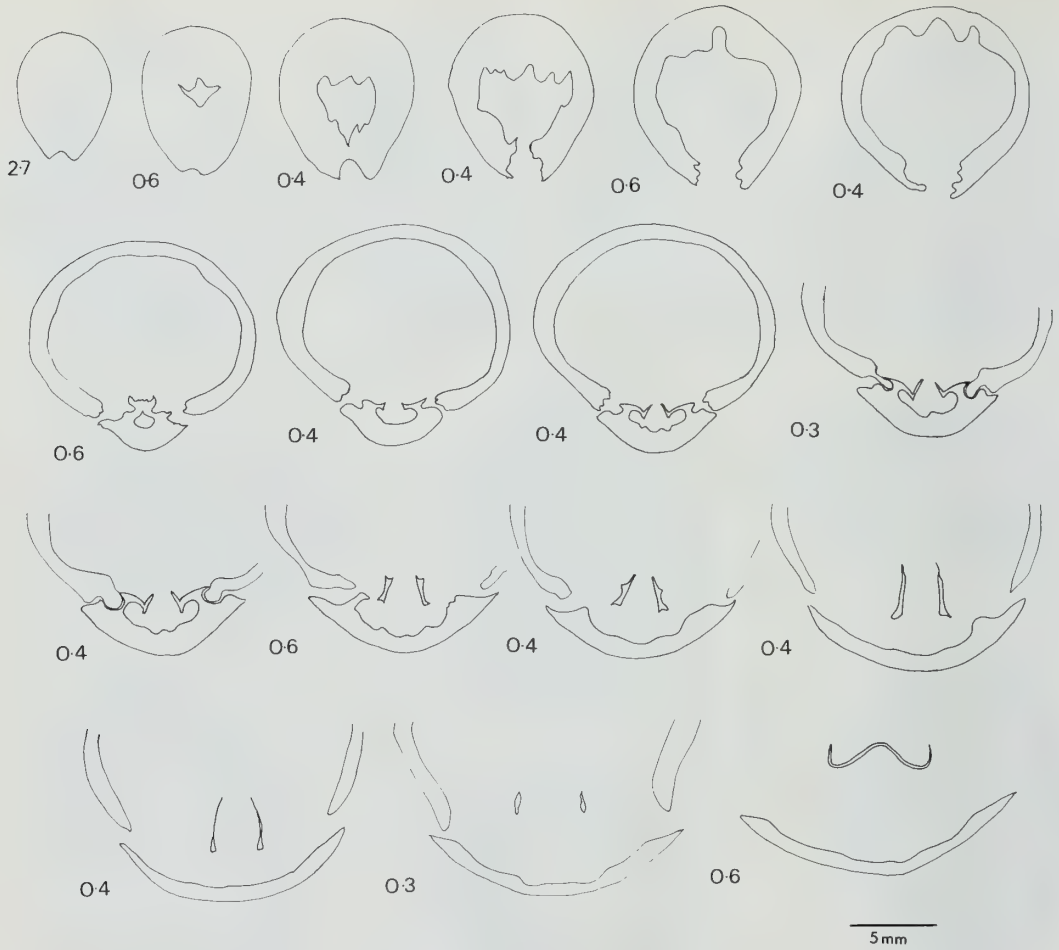

Fig. 23 *Concinnithyris obesa* (J. de C. Sowerby). Seventeen transverse serial sections through BB82332, from the Lower Chalk, 1 m above the Cenomanian Basement Bed, White Nothe, Dorset.

Remarks. Sahni (1929: 12) gave an adequate description of the species based on the Sowerby type and accompanied this with two dissected specimens (1929: pl. 8, figs 1–2), one of which, B49884, he called a plesiotype from 'The Chalk' of Lewes, Sussex. This specimen, from an unspecified horizon within the Chalk, should only be assigned to *Concinnithyris obesa* (J. de C. Sowerby) with doubt.

Sahni did not recognize variability in the species and so considered only large, almost perfect, but miserably few, specimens matching the holotype as representative of *C. obesa*. In fact, thorough investigation of specimens collected from the Lower Chalk of Dorset, Wiltshire and the Isle of Wight shows that the range of variation includes specimens which do not match the holotype in their general dimensions; these may be steeper-flanked and with subparallel outlines, may be anteriorly constricted and also less acutely biconvex. A range of variants representing the species is figured here (Pl. 14, figs 1–15), including the holotype (figs 1–3).

Specimens from a bed less than one metre above the phosphatic conglomerate comprising the Cenomanian Basement Beds are always highly calcareous, non-phosphatized, and whitish in colour. This bed occurs extensively at Snowdon Hill, Chard, Somerset; White Nothe, Ringstead and Durdle Cove, Dorset; Charstock, Devon; and in the Isle of Wight. From amongst

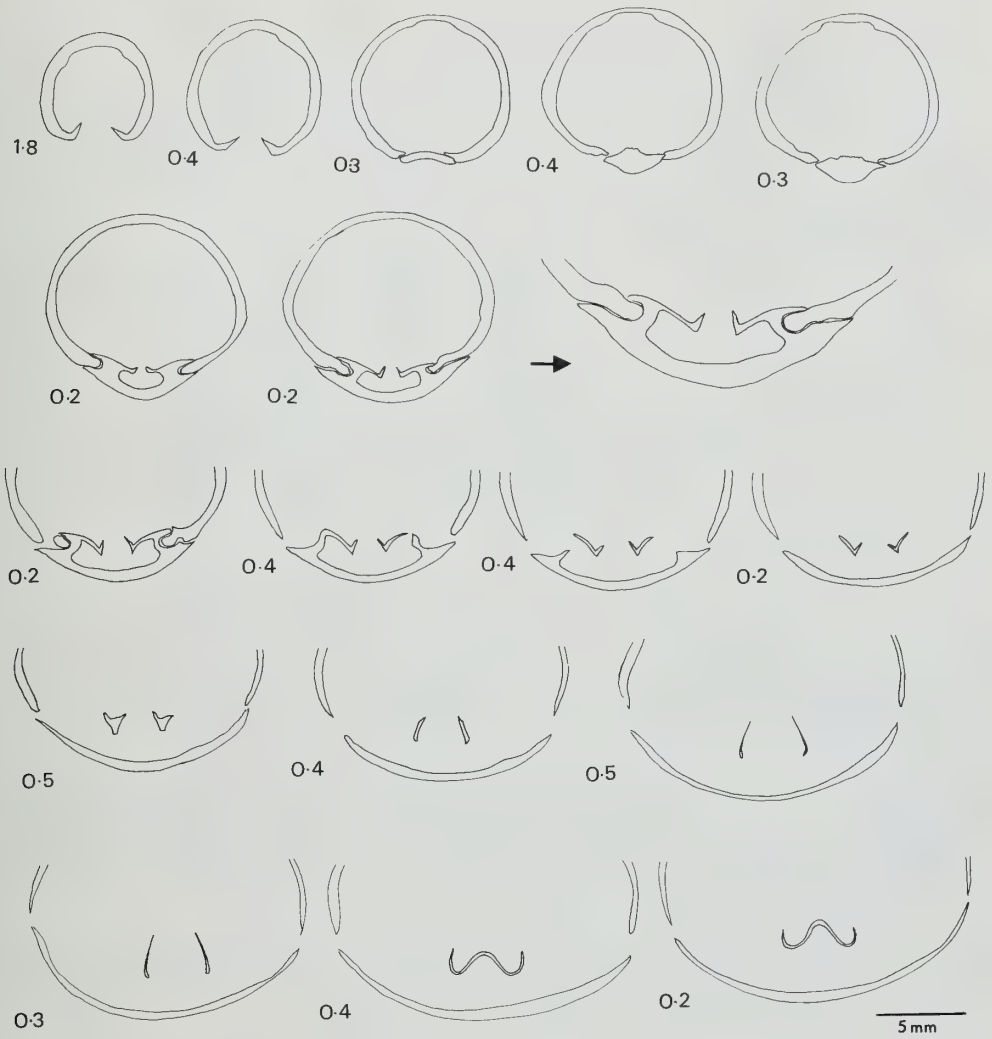

Fig. 24 *Concinnithyris davidsoni* (Rollier). Seventeen serial sections through B5070, from the Upper Greensand of Warminster, Wiltshire. One section also shown at greater enlargement.

such specimens a variant is recognized by its flatter valves, large foramen, and more acute biplication of the anterior commissure.

All variants, including specimens like the type, have been recognized in collections from the Craie de Rouen, France, from where the species was collected and described by d'Orbigny (1850) as from his 'Étage Turonien'. Since the work of Kennedy & Hancock (1970), Juignet & Kennedy (1976) and others, it is now known that the Craie de Rouen is of Middle Cenomanian age.

Davidson (1852: 53; pl. 5, figs 13–15) interpreted *C. obesa* as the biplicate terebratulid which occurs rarely in the Warminster Greensand. Apart from their large size the two forms are dissimilar and it seems strange that Davidson should have made this decision, especially since Sowerby's original specimen of *T. obesa* was available to him. Because of this misinterpretation Rollier (1911: 28) changed the name of the Warminster species to *Terebratula davidsoni*, and

this species occurs also in the Tourtia of Tournai, Belgium (Pl. 11, figs 10–12). It has been confused with *Terebratula sabinensis* Parent, 1893 (Pl. 11, figs 1–3), which should probably be placed in *Ornatothyris*. *T. sabinensis* differs from *C. davidsoni* in its evenly oval outline, suberect and truncated umbo and lack of biplication of the anterior commissure.

Transverse serial sections through a young specimen of *Concinnithyris davidsoni* (Fig. 24) display the comparatively short ventrally deflected inner hinge-plates, the long incurved crural processes and the low W-shaped transverse band of the brachial loop, and should be compared with the series for the type species (Fig. 23).

DIMENSIONS. Measurements in mm.

Locality	number	length	width	thickness
Isle of Wight	BB69017	28·9	23·9	19·3
	BB82080	44·8	33·3	34·9
Ringstead	BB69013	32·1	24·8	21·0
Osmington	BB45120	45·2	35·8	33·1
Durdle Cove	BB69088	30·4	23·1	20·5
	BB69085	30·7	26·0	19·6
Snowdon Hill	BB82364	40·6	34·9	26·1
	BB82365	31·8	29·2	20·5
	BB82366	29·4	23·9	18·7
Rouen, France	BB82367	44·9	38·6	34·4

Concinnithyris subundata (J. Sowerby)

Figs 25–27; Pl. 6, figs 16–18; Pl. 15, figs 4–18; Pl. 16

1813 *Terebratula subundata* J. Sowerby: 47; pl. 15, fig. 7.
1929 *Concinnithyris subundata* (J. Sowerby) Sahni: 17; pl. 1, figs 10–16 (*non* fig. 17); pl. 8, figs 11–12.
1929 *Concinnithyris subundata* (J. Sowerby) Sahni: 17; pl. 1, figs 10–16 (*non* fig. 17); pl. 8, figs 11–12.
1929 *Concinnithyris burhamensis* Sahni: 16; pl. 2, figs 8–13; pl. 8, figs 22–23.

EMENDED DESCRIPTION. The beak is suberect epithyridid with a modest circular foramen. Symphytium not exposed. The outline of the shell varies from subpentagonal (Pl. 15, fig. 4) to subcircular (Pl. 15, fig. 13), to elongate-oval (Pl. 16, fig. 1). An even greater degree of biconvexity is common for adults, but diminishes in some variants. Rarely a shallow dorsal median sulcus occurs, usually bordered by faint carinae, forming a weakly biplicate anterior commissure, which otherwise is gently uniplicate.

INTERNAL CHARACTERS. Apart from the early stages in the development of the hinge-plates, and their shorter length than those of the type-species, other internal features closely resemble those of *C. obesa*; compare Fig. 23 with Fig. 25.

LECTOTYPE. Sowerby Collection, B49827, figured by J. Sowerby 1813: pl. 15, fig. 7 (Pl. 16, figs 1–3). Herein selected.

Sowerby's (1813: 47) original description appears to have been based on several specimens, but illustrated by only one (1813: pl. 15, fig. 7), a strongly biconvex, elongate specimen having, according to Sowerby, 'a fleshy red colour'. Today there are six specimens named *C. subundata* in the Sowerby Collection (B49826–31). When Sahni (1929) included this species in his new genus *Concinnithyris* he selected as what he called a 'Neanic Holotype' specimen B49826 (Pl. 15, figs 1–3), but mentioned no other Sowerby specimen as any part of a type series. This specimen closely resembles neither the above original Sowerby figure nor most of Sahni's own illustration of the species (1929: pl. 1, figs 10–15). In addition the matrix is glauconitic, and it is thus probably from the Chalk Rock rather than from the 'softish Chalk at Warminster' (Sowerby 1813), which is probably Lower Chalk in that area.

Specimen B49827 resembles Sowerby's fig. 7 more closely than does B49826. It also fulfills most of Sahni's own criteria for his description of *C. subundata*, as well as matching his illustrations (1929: pl. 1, figs 10–15). The species is well known from the Lower Chalk, from which specimen B49827 probably came, and for these reasons I select it as Lectotype of *C.*

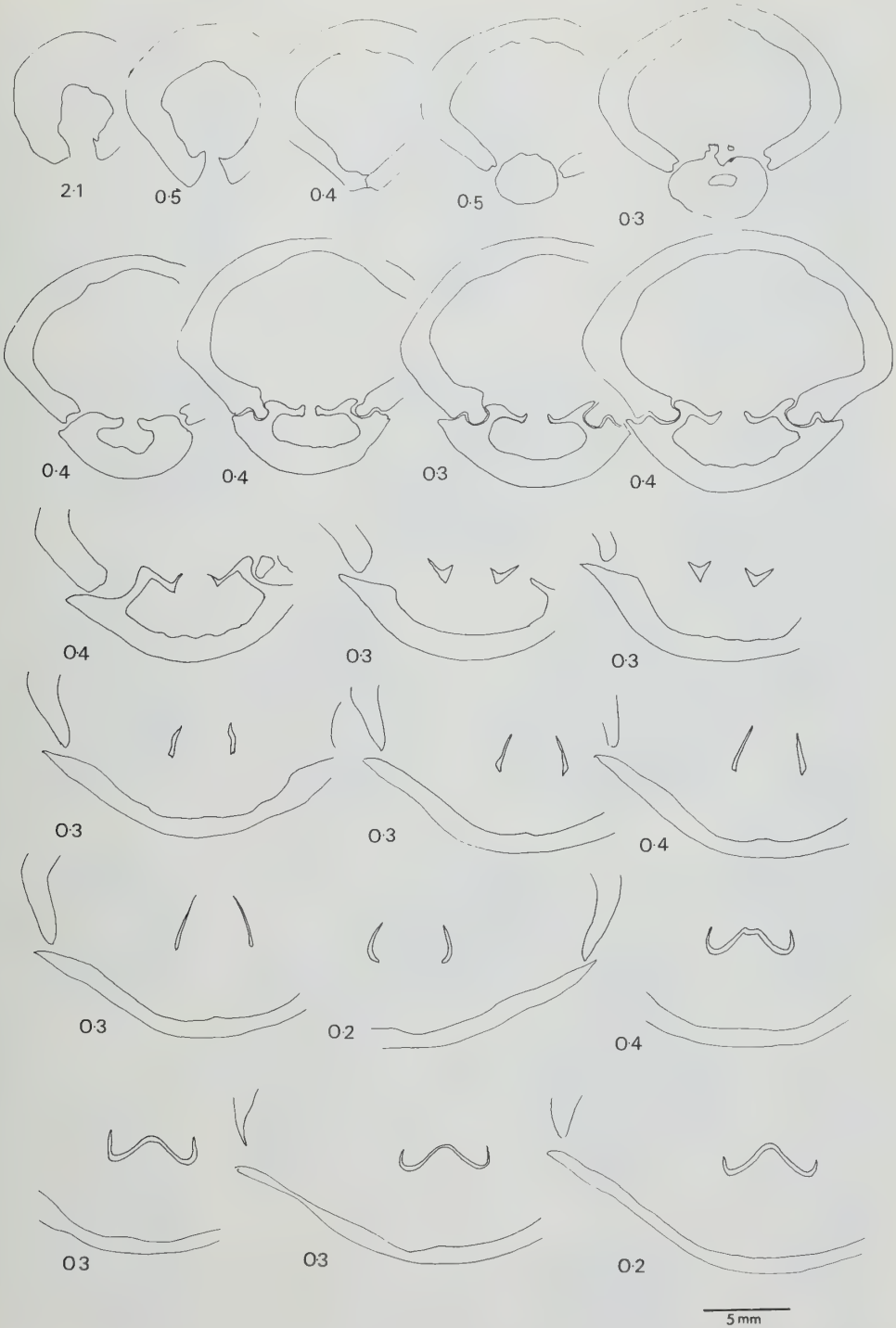

Fig. 25 *Concinnithyris subundata* (J. Sowerby). Twenty-one transverse serial sections through BB82335, from the Lower Chalk, Southerham Gray Pit near Lewes, E. Sussex.

subundata (J. Sowerby). The specimen is not now flesh coloured, but such colouration tends to fade from newly collected specimens.

REMARKS. Measurements of specimens from the Basement Beds in Dorset and Wiltshire, and some from French localities, reveal that in many there is considerable variation in the size of the foramen. In addition these specimens tend to be less biplicate or have a simple uniplicate anterior commissure. As far as can be detected from the comparatively few that have been serially sectioned, these differences are not reflected internally.

DIMENSIONS of BM(NH) specimens. Measurements in mm.

Number	length	width	thickness
Burham, Kent:			
B9449	33·4	26·1	22·1
B9450	34·4	26·2	22·1
B9455	32·8	29·1	18·2
B9460	26·8	25·2	18·2
Folkestone, Kent:			
B22876	30·4	26·3	19·2
BB5602	30·5	25·4	19·5
BB5603	34·1	27·2	20·5
Oxted, Surrey:			
B58233	37·6	31·3	22·9
B44820	30·1	27·1	18·2
B44822	29·1	25·2	18·2
Chinnor, Oxon:			
B47274	31·5	26·5	19·0
Guildford, Surrey:			
B10634	29·3	25·4	15·4
Culver, Isle of Wight:			
BB68996	39·4	33·8	22·0
BB81153	35·7	29·0	20·3
Punfield, Dorset:			
BB69104	30·8	26·2	18·2
Evershot, Dorset:			
BB82163	32·5	28·0	20·9
BB82164	29·8	25·5	19·2
BB82165	32·7	28·7	22·8
BB82166	30·5	24·1	18·4
Burwell, Cambridge:			
B24968	32·1	26·7	16·8
„	27·7	25·0	16·1
„	26·7	24·5	16·9
Rouen, France:			
B35074	26·0	22·9	16·6
„	26·3	23·1	15·6
BB82167	28·6	25·3	18·0
St Jouin, Normandy:			
BB82168	29·8	25·8	18·9
BB82169	25·4	22·7	14·5

C. subundata also occurs in the Grey Chalk and the Grey/Red Chalk of Speeton, Yorkshire and examples from the BM(NH) collections are BB43357–59, BB45141–49, BB69113–17, BB69119, BB69147–59 and BB82774–809.

Genus *ORNATOTHYRIS* Sahni, 1929

TYPE SPECIES. *Terebratula sulcifera* Morris, *in* Davidson & Morris 1847.

REMARKS. In his original description of the genus, Sahni (1929) gave the geological range as Cenomanian–Senonian. Within the nine species he described he distinguished two morphological groups by differences in rugose shell ornamentation. One group, which he termed 'totirugose', included all the Cenomanian species in which both valves are covered by prominent

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PLATE 13

Figs 7–9 *Ornatothyris sulcifera* (Morris). Cenomanian, Fulbourn, Cambridge. BB6017, × 1½.
Figs 1–3, 10–12 *Ornatothyris* cf. *sulcifera* (Morris). Figs 1–3, Cenomanian, Cassis, southern France. BB82174, × 1½. Figs 10–12, Middle Cenomanian, Grove Mill Pit, Hitchin, Herts. BB82190, × 1½.
Figs 4–6, 13–18 *Ornatothyris* sp. Figs 4–6, Craie de Rouen, Côte Ste Catharine, Rouen. BB82200, × 1½. Figs 13–18, Brunni Alp, Bernese Oberland, Switzerland. Geneva Nat. Hist. Mus. Figs 13–15, C.B. 366, × 1½. Figs 16–18, C.B. 369, × 1½.

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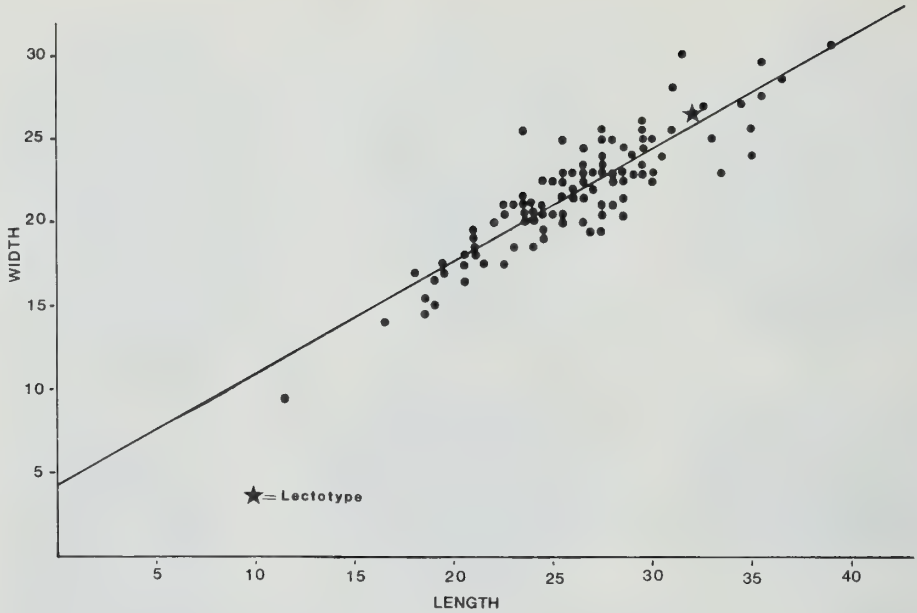

Fig. 26 Length × width graph and regression line for 102 specimens of *Concinnithyris subundata* (J. Sowerby) from England.

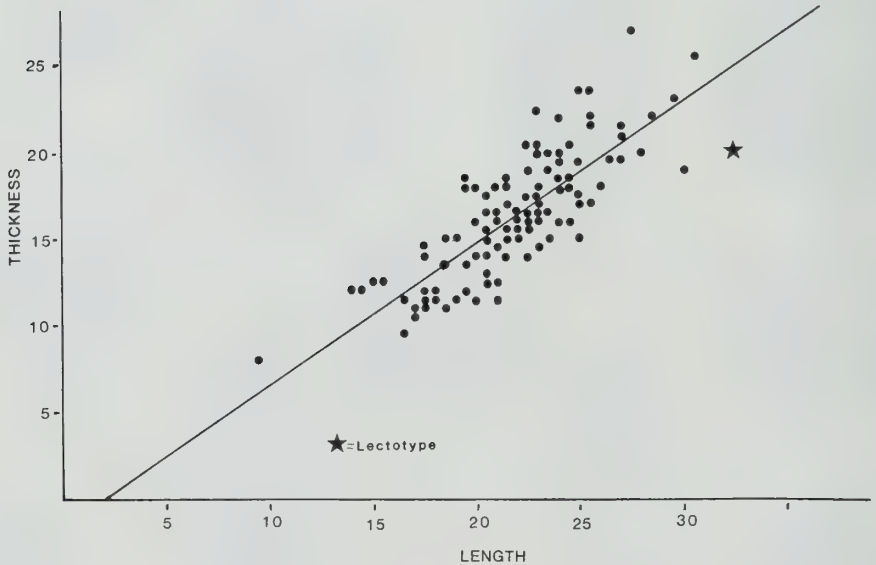

Fig. 27 Length × thickness graph and regression line for 102 specimens of *Concinnithyris subundata* (J. Sowerby) from England.

PLATE 14

Figs 1–15 *Concinnithyris obesa* (J. de C. Sowerby). Figs 1–3, Lower Chalk, Norton Bavant, Wiltshire. Holotype B49832, × 1. Figs 4–6, Craie de Rouen, Côte Ste Catharine, Rouen. BB84903, X1. Figs 7–9, Middle Cenomanian, Ringstead, Dorset. BB45120, × 1. Figs 10–12, Craie de Rouen, Rouen. B5101, × 1. Figs 13–15, Middle Cenomanian, Isle of Wight. BB84904, × 1.

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growth-lines. His second group, which included all the species from the *Micraster coranguinum* Zone of Greenhithe, Kent, was termed 'partirugose' because this ornamentation was present only anteriorly.

Five of the six totirugose species came from the Cambridge district; the sixth was said to have come from an unknown locality but a second specimen was figured from Warminster, B49828, a locality from which the genus has never since been recorded. Although somewhat vague, the localities quoted by Sahni from the Cambridge area are reasonably recognizable, but it is not known for certain from exactly which horizon each of Sahni's holotypes originates. The Lower Chalk of the Cambridge district covers many of the zones within the Cenomanian, the lowest part being represented by the Cambridge Greensand, considered to be of *carcitanense* equivalent age, i.e. lowest Cenomanian (Carter & Hart 1977: 75). The highest level ranges to the Plenus Marl.

It is likely that *O. sulcifera* is a variable species and that most of Sahni's other species from the same Cambridge area are merely variants. The possible exceptions are *O. pentagonalis* and *O. latissima*, which appear as consistent morphological forms; in particular *O. pentagonalis* (Pl. 12, figs 13–15) is found in the '*Paradoxica*' Bed of the 'White Chalk' of Hunstanton Cliff, i.e. low in the succession. *O. latissima* (Pl. 12, figs 1–3), on the other hand, appears to be the dominant species of an assemblage containing remanié *Orbirhynchia multicostata* and *Monticlarella jefferiesi* in pockets of green clay in the conglomeratic erosion surface below the Black Band at Elsham and Caistor in Lincolnshire, and at Hillington and Heacham in Norfolk. This is high in the succession, in the top part of Bed IX of Bower & Farmery (1910) in the upper *Holaster trecensis* Zone.

Ornatothyris differs from *Concinnithyris* externally by having a clearly developed ornament of rugose concentric growth-lines. Internally it differs in its less developed cardinal process, shorter and thicker hinge-plates, and dorsally pendant and shorter brachial loop. It also differs in this way from *Moutonithyris*, but *Terebratula obtusa* J. de C. Sowerby (1825) from the Cambridge Greensand, and previously called *Ornatothyris obtusa*, is here assigned to *Moutonithyris*: see p. 122.

Ornatothyris sulcifera (Morris)

Fig. 28; Pl. 13, figs 1–3, 7–12

1847 *Terebratula sulcifera* Morris, *in* Davidson & Morris: 354; pl. 18, fig. 7.
1855 *Terebratula sulcifera* Morris; Davidson: 64; pl. 7, figs 17–20.
1929 *Ornatothyris sulcifera* (Morris) Sahni: 48; pl. 7, figs 1–10; pl. 10, figs 25–27.

HOLOTYPE. Davidson Collection, 50822; from the Lower Chalk; near Cambridge.

REMARKS. Sahni figured four specimens from the Lower Chalk of Fulbourn (1929: 48) to illustrate the species. Another Fulbourn, Cambridge specimen, said to have been collected from the *subglobosus* Zone by L. Barrett, is 36·2 mm long, 28·0 mm wide and 23·2 mm thick (BB6017; Pl. 13, figs 7–9).

The species appears to be confined to eastern England and Cassis, southern France, where specimens occur in Lower Cenomanian ironstained limestone deposits. One of these (BB82147) is figured (Pl. 13, figs 1–3); it is 30·4 mm long, 26·7 mm wide and 18·9 mm thick. It is broader

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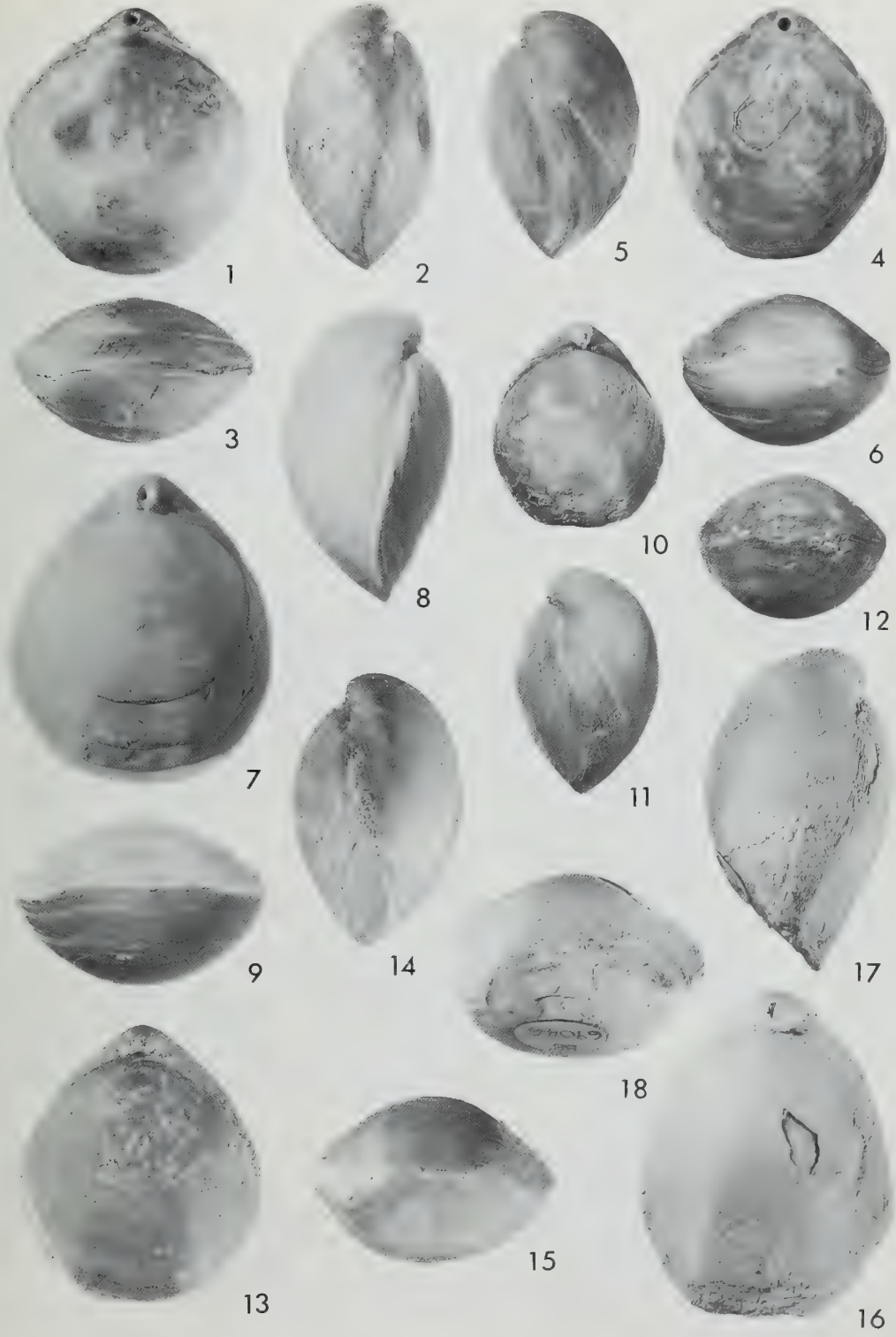
PLATE 15

Figs 1–15 *Concinnithyris subundata* (J. Sowerby). Figs 1–3, specimen suggested by Sahni (1929) as lectotype of this species, but not here accepted. ?Chalk Rock (see p. 132). Sowerby colln, B49826, × 1½. Figs 4–6, Middle Cenomanian, Oxted, Surrey. B44830, × 1½. Figs 7–9, large example from Lower Chalk, Burham, Kent. 96789, × 1½. Figs 10–12, Chalk Basement Bed, Snowdon Hill, Chard, Somerset. BB82171, × 1½. Figs 13–15, Craie de Rouen, Côte Ste Catharine, Rouen, France. BB82167, × 1½.

Figs 16–18 *Concinnithyris* cf. *subundata* (J. Sowerby). Cenomanian, Grey/Red Chalk, Speeton Cliff, N. Yorkshire. BB69046, × 1½.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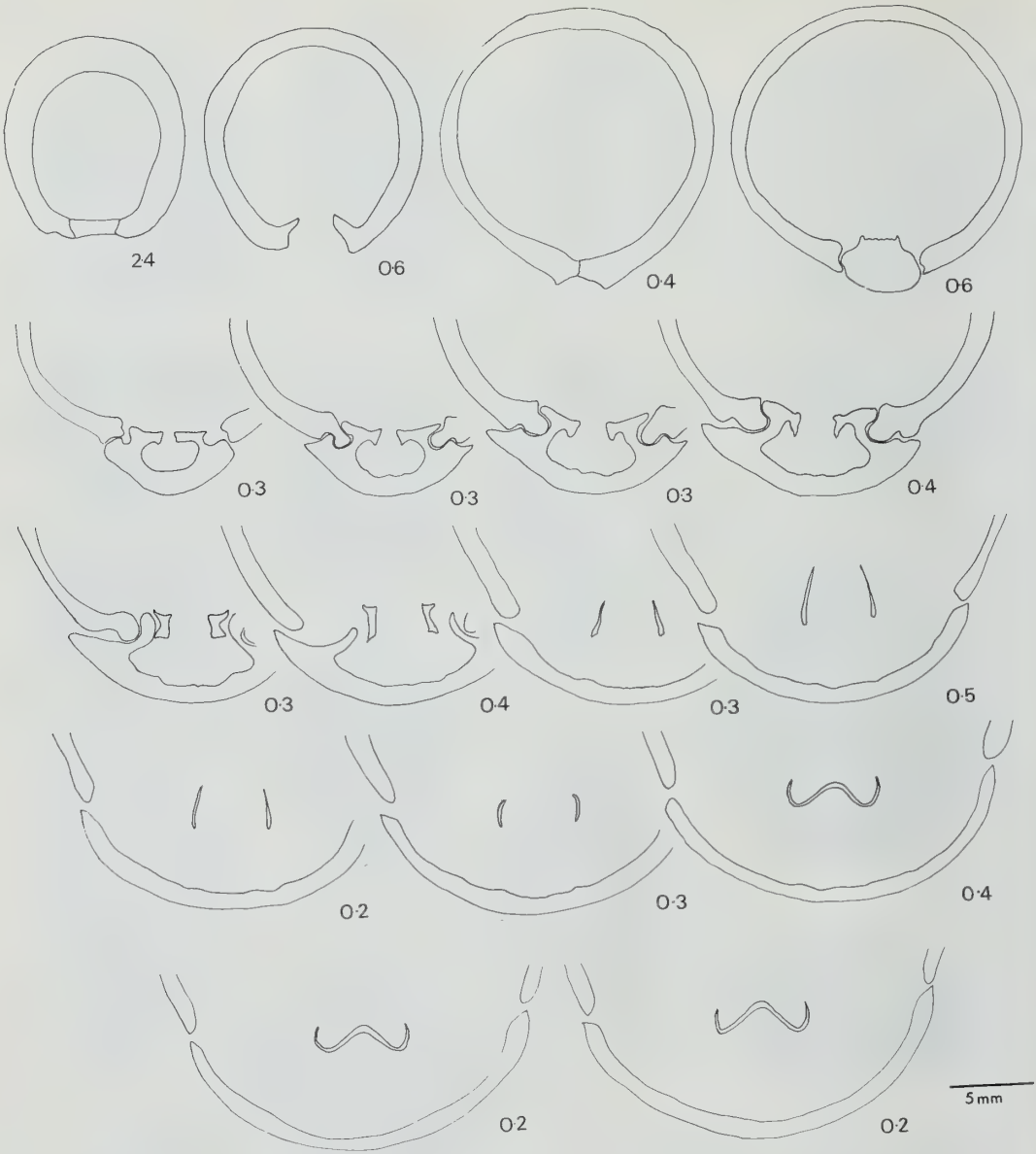

Fig. 28 *Ornatothyris sulcifera* (Morris). Seventeen transverse serial sections through BB82338 from the Lower Chalk, Fulbourn, Cambridge.

PLATE 16

Figs 1–12 *Concinnithyris subundata* (J. Sowerby). Figs 1–3, **lectotype**, here selected. ?Lower Chalk (see p. 132). Sowerby colln, B49827, × $1\frac{1}{2}$. Figs 4–6, Eggardon Grit, Eggardon Hill, Dorset. BB82170, × $1\frac{1}{2}$. Figs 7–9, Middle Cenomanian, Glynde, E. Sussex (*C. burhamensis* aspect). BB82347, × $1\frac{1}{2}$. Figs 10–12, Grey/Red Chalk, Speeton Cliff, N. Yorkshire. BB84906, × $1\frac{1}{2}$.

Figs 13–15 *Concinnithyris* cf. *subundata* (J. Sowerby). Pit 3, Hallington, Louth, Lincolnshire. B55145, × $1\frac{1}{2}$.

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and more circular in outline and has more numerous, evenly spaced growth-lines than the holotype; the umbo is also more massive than in typical *O. sulcifera* or any other species within the genus. The circular foramen is perhaps slightly proportionately larger with a marked pedicle collar.

A British specimen collected by C. J. Wood, from the upper third of the *subglobosus* Zone of Grove Mill Pit, Cadge Lane, Hitchin, Hertfordshire, is similar to the Cassis specimens in outline, convexity and type of concentric ornament, but differs in having a less massive umbo which is truncated by a large circular foramen. This specimen is 25·0 mm long, 22·3 mm wide and 15·7 mm thick.

INTERNAL CHARACTERS. Seventeen transverse sections (Fig. 28) through an unregistered specimen from the Lower Chalk of Fulbourn, Cambridge, display a well developed pedicle collar guarding a large foramen in the ventral umbo. Short, thickened horizontal hinge plates flatten proximally and curve gently towards the floor of the dorsal valve, developing short pendant plates which thicken anteriorly, turning into long, slender, inwardly curving crural processes. The comparatively short brachial loop widens very slightly, terminating in a broad, high-arched transverse band.

The hinge-plates have very strong inner but weaker outer socket-ridges. The hinge-teeth fit into shallow, rounded sockets.

Subfamily **CAPILLITHYRIDINAE** Cooper, 1983

Genus ***CAPILLITHYRIS*** Katz, 1974

Capillithyris squamosa (Mantell)

Pl. 18, figs 14–16; Pl. 27

1822 *Terebratula squamosa* Mantell: 132.
1847 *Terebratula squamosa* Mantell; Davidson & Morris: 254; pl. 18, figs 8, 8a, 8b.
1847 *Terebratula disparilis* d'Orbigny (*pars*): pl. 512, fig. 17 only.
1852 *Terebratula squamosa* Mantell; Davidson (*pars*): 50; pl. 5, figs 5, 6 only.
1874 *Terebratula squamosa* Mantell; Davidson: 33; pl. 2, fig. 5.
1978 *Platythyris squamosa* (Mantell) Middlemiss: 39, figs 11, 12, 16 (9).

HOLOTYPE. Mantell Collection, B8292; from the Chalk Marl of Hamsey, near Lewes, Sussex.

REMARKS. Middlemiss (1978) fully described this species in his paper on the genus *Platythyris* so no further description is necessary here.

There has been some confusion between this species and *Arcuatothyris arcuata* (Roemer), p. 144, since both occur in the more highly calcareous beds in southwestern England, particularly in the phosphatic basement beds of the B group on the coast of south Devon. This confusion is made worse by the presence of a third species, which is also somewhat homo-

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PLATE 17

Figs 1–3 *Gemmarcula carantonensis* (d'Orbigny). Upper Cenomanian, Port des Barques, Charente, France. BB45960, × 2.

Figs 4–6 *Gemmarcula menardi* (Lamarck). Sable du Mans, Le Mans (Sarthe). BB35152, × 2.

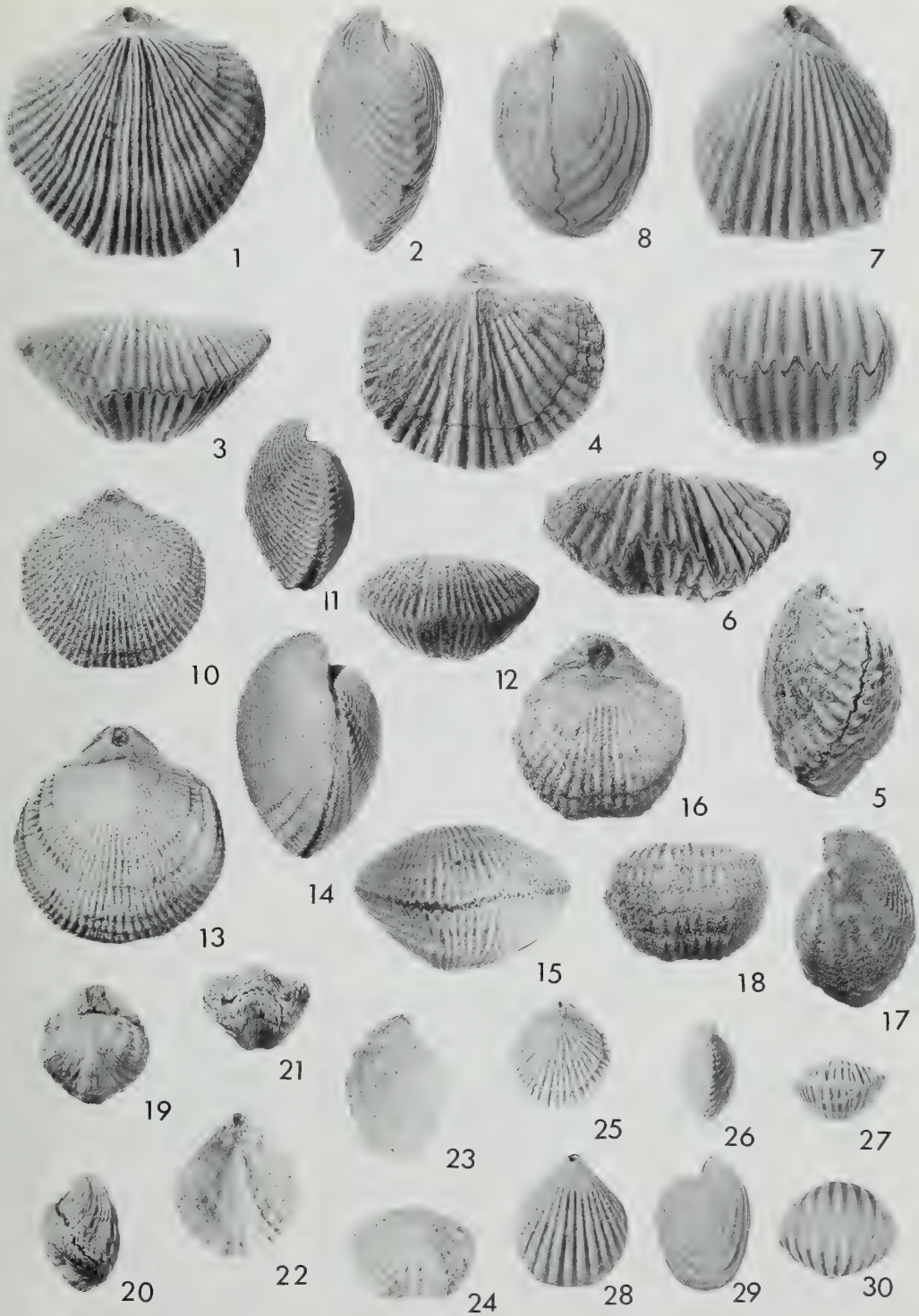
Figs 7–9, 28–30 *Arenaciarcula beaumonti* (d'Archaic). Figs 7–9, Cenomanian, Drap, near Nice. BB85424, × 1½. Figs 28–30, Tourtia, Tournai, Belgium. BB45970, × 2.

Figs 10–15 *Dereta pectita* (J. Sowerby). Figs 10–12, ?Middle Cenomanian, near Warminster, Wiltshire. B25263, × 2. Figs 13–15, Upper Greensand, from type locality at Horningsham, Wiltshire. BB4199, × 1½.

Figs 16–18 *Dereta pectita ballardensis* subsp. nov. Upper Albian, *S. dispar* Zone, Ballard Point, Swanage, Dorset. **Holotype** BB82098, × 2.

Figs 19–24 *Gemmarcula canaliculata* (Roemer). Figs 19–21, Tourtia, Tournai, Belgium. BB82191, × 1½. Figs 22–24, Lower Cenomanian, White Hart sand pit, Wilmington, Devon. BB82193, × 2.

Figs 25–27 *Dereta incerta* (Davidson). Glauconitic Marl, Chardstock, Devon. BB84907, × 2.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eomorphic: it was described as a subspecies *Platythyris squamosa disparilis* (d'Orbigny) by Middlemiss (1978), but I consider it a true species *C. disparilis*. *C. squamosa* can be distinguished from *C. disparilis* by its flatter valves, wider hinge-line and less massive umbo which is truncated by a comparatively large circular foramen. The outline of *C. squamosa* is oval, although many individuals display an anterior tapering of the valves.

Both species have a marked ornament of growth-lines which are evenly spaced and show unusual cuspidate leading edges (Pls 27, 28) and impersistent fine longitudinal striae: in the larger *C. disparilis*, this ornament tends to become more zigzag towards the margins of the shell (Pl. 28, figs 3, 4). This characteristic ornament distinguishes *Capillithyris* from *Arcuatothyris*, and is particularly useful since *C. squamosa* resembles *Arcuatothyris arcuata* (Roemer) in outline. The former has flatter valves and lacks an anterior sulcation of the brachial valve, a feature of Roemer's original illustration (Roemer 1841: pl. 8, figs 18a–c).

Family ?**BOREIOTHYRIDAE** Dagys, 1968

Genus ***ARCUATOTHYRIS*** Popiel-Barczyk, 1972

Arcuatothyris arcuata (Roemer)

Pl. 26

1841 *Terebratula arcuata* Roemer: 44; pl. 8, figs 18a–c.
1847 *Terebratula rugulosa* Morris, *in* Davidson & Morris: 153; pl. 18, figs 5a–c.
1847 *Terebratula disparilis* d'Orbigny: 100; pl. 512, figs 12, 13, *non* figs 16, 17.
1852 *Terebratula rugulosa* Morris; Davidson: 49; pl. 4, figs 14, 14a.
1866*a* *Terebratula arcuata* Roemer; Schloenbach: 451; pl. 21, fig. 12.
1878 *Terebratula arcuata* Roemer; Deike: 15, figs 6a–d.
1969 *Terebratella arcuata* (Roemer) Panow: 594; pl. 110, figs 8, 9.
1970 *Terebratula rugulosa* Morris; Kennedy: 634, 660.
1974 *Arcuatothyris arcuata* (Roemer) Katz: 268; pl. 87, figs 18a–d, 20a–c.
1978 *Terebratula rugulosa* Morris; Owen: 148, 151.
1978 *Terebratula rugulosa* Morris; Middlemiss: fig. 16, 3a–d.

Type specimen. Roemer's original type specimen is missing but it seems likely from his drawings (Roemer 1841: pl. 8, figs 18a–c) that the species is a senior synonym of *T. rugulosa* Morris, 1847. If a neotype is to be considered it should come from the conglomeratic horizon known as the Essen Greensand.

As the presumed junior synonym *Terebratula rugulosa* Morris, the species is known in Britain from the Glauconitic Marl of Chardstock, Devon, the holotype being in the Davidson Collection, B6130; it was refigured by Davidson (1852: pl. 4, fig. 14) and Middlemiss (1978: fig. 15/2).

Remarks. The species can be distinguished from *Capillithyris squamosa* (Mantell) by its steeper flanks, and shallow sulcus anteriorly on the brachial valve. It differs from *Ovatathyris ovata* in

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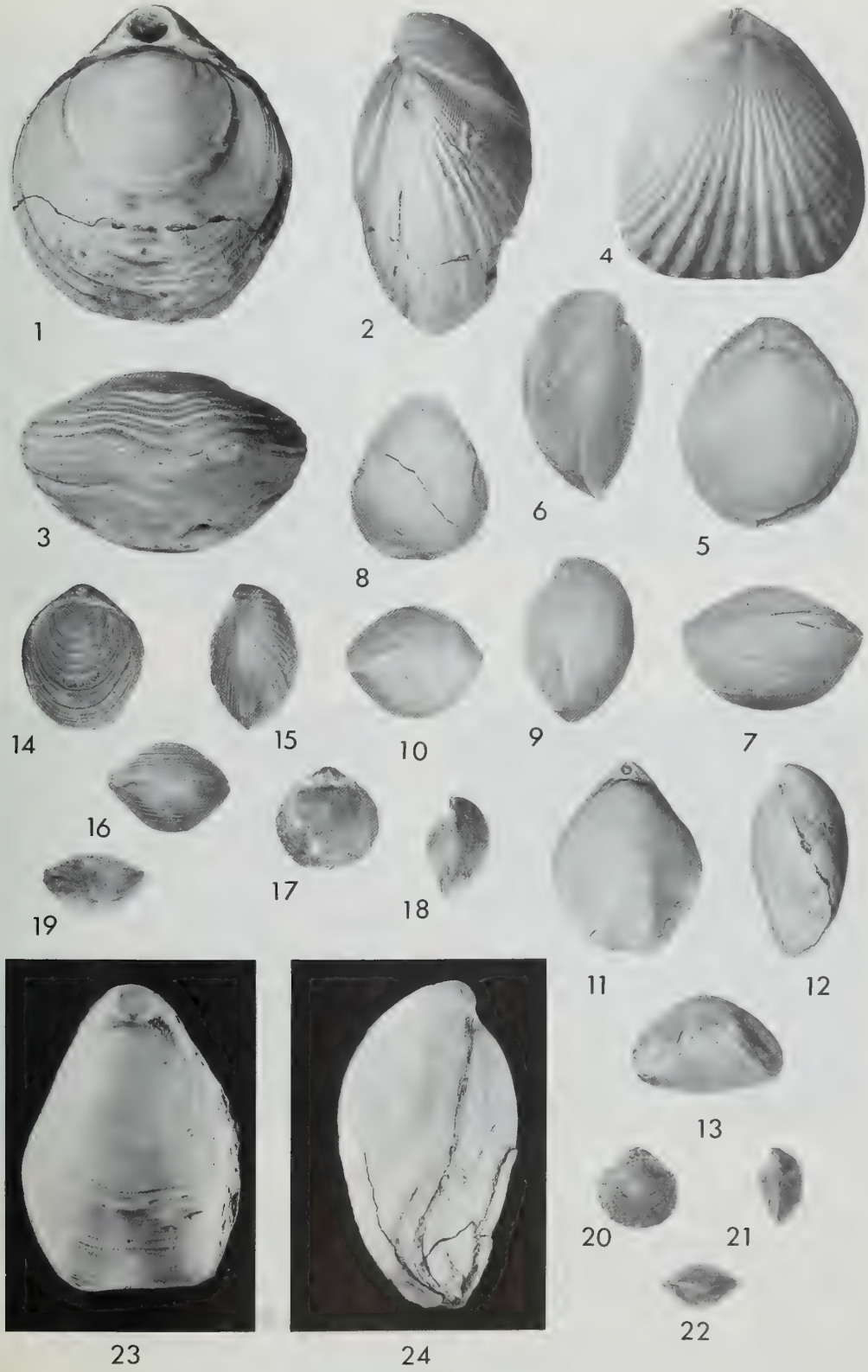
PLATE 18

Figs 1–3 *Capillithyris capillata* (d'Archaic). Tourtia, Tournai, Belgium. B46351, × $1\frac{1}{2}$.
Fig. 4 *Monticlarella brevirostris* (Roemer). Chalk Marl, Folkestone. 82144, × 5.
Figs 5–10 *Concinnithyris* sp.? Two similar specimens. Figs 5–7, Bed B, Red Rock, Hunstanton, Norfolk. BB82145, × 2. Figs 8–10, Lower Cenomanian, Brockterbek, north Germany. BB82146, × 2.
Figs 11–13 *Sellithyris* cf. *phaseolina* (Valenciennes, *in* Lamarck), possibly an elongated variant. Upper Cenomanian, Charente. BB82212, × $1\frac{1}{2}$.
Figs 14–16 *Capillithyris squamosa* (Mantell). Lower Chalk, St Jouin, Normandy. BB85611, × $1\frac{1}{2}$.
Figs 17–22 *Modestella geinitzi* (Schloenbach). Figs 17–19, Lower Chalk, Folkestone. BB82214, × 2. Figs 20–22, Essen Greensand, Essen, Germany. BB82213, × 2.
Figs 23–24 *Moutonithyris dutempleana* (d'Orbigny). Upper Gault, Price's Bed X, Folkestone. Fig. 23, B1132, × $1\frac{1}{2}$. Fig. 24, B2231, × $1\frac{1}{2}$.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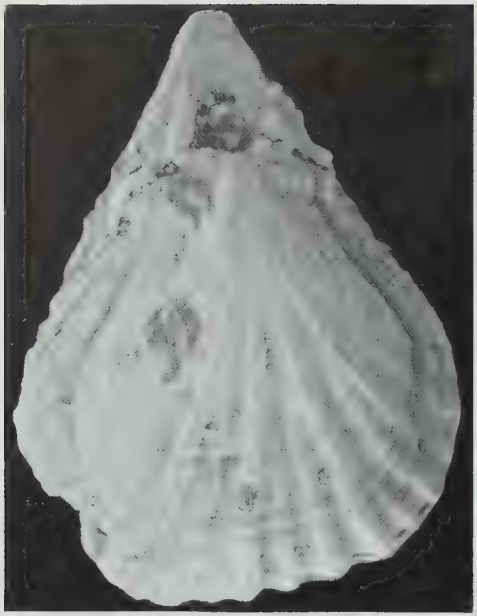

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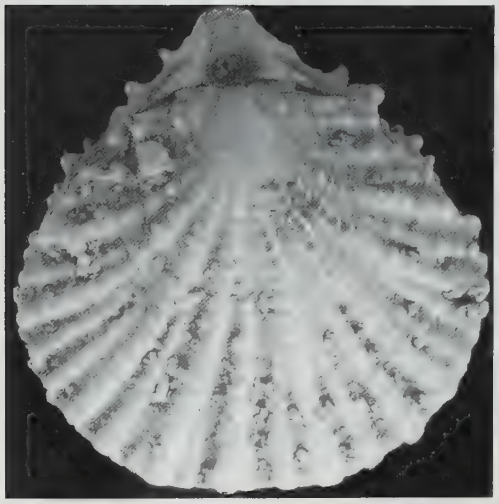

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PLATE 19

Figs 1–4 Immature *Terebratulina* spp. Cambridge Greensand, Cambridge. Figs 1–2, thought to be *T. etheridgei* nom. nov. (= *T. triangularis* Etheridge, *non* Tate). B7021, SEM × 40. Figs 3–4, thought to be *T. nodulosa* Etheridge. BB82353 and 82354 respectively, SEM × 35.

its general outline and lack of ventral carina, poorly defined beak-ridges, smaller foramen and less marked brachial sulcus. It differs from both these species in its characteristic shell ornament of spinules which are arranged roughly radially over the surface of the valves (Pl. 26, figs 1–4) but with areas between some growth-lines devoid of spinules. These are thought to represent times when growth at the mantle edge was too rapid for the development of spinules. This ornament differs from that of *Ovatathyris* in its distribution over the surface of the shell. In *A. arcuata* the spinules are more strongly developed and interdigitate, whereas in *Ovatathyris* they do not normally overlap with those from adjacent bands.

This species occurs with *Capillithyris squamosa* and *C. disparilis* in the phosphatic chalky conglomerates of the Basement Beds of the Lower Chalk at Evershott, Eggardon Hill, Toller Porcorum, Toller Fratrum and Beaminster, Dorset; and at Bovey Lane, Wilmington sand pit and from the coastal sections at Humble Point and the Pinnacles, Devon, where it occurs in Beds B and C of the Cenomanian.

MATERIAL. Abundant material from the above localities is in the Kennedy Collection, BM(NH). Additional material includes: BB76507 from the Glauconitic Marl, Chardstock, Devon; BB82221–5 from the Lower Chalk Basement Bed, Snowdon Hill, Chard, Somerset; BB82361 from Horn Hill Quarry, Beaminster; BB82362–5 from the White Hart sand pit, Wilmington; BB82260 from Hutchin's Pit, Wilmington, Devon; and B6131 from the Craie de Rouen, Côte Ste Catharine, Rouen, France.

Family **CANCELLOTHYRIDIDAE** Thomson, 1927

Subfamily **CANCELLOTHYRIDINAE** Thomson, 1927

Genus ***TEREBRATULINA*** d'Orbigny, 1847

Terebratulina etheridgei nom. nov.

Pl. 5, fig. 17; Pl. 19, figs 1, 2

NOM. NOV. *pro Terebratulina triangularis* Etheridge, 1881: 148; pl. 13, fig. 15; *non Terebratulina triangularis* Tate, 1880: 160; pl. 8, fig. 7.

HOLOTYPE. Jukes-Browne Collection, BGS no. 3156; from the Cambridge Greensand.

REMARKS. Unfortunately, Etheridge's original species name *Terebratulina triangularis* had previously been used by R. Tate to describe a species from the Lower Tertiary of South Australia, so although long used to describe specimens from the Cambridge Greensand, it must now be changed.

The species can be distinguished from other *Terebratulina* species by its consistently triangular outline. This is very largely on account of the slightly more extended hinge-line which adds greatly to the posterior width of the shell and increases the interarea. It can be further distinguished from *T. imbricata* sp. nov. (p. 148) in having non-lamellose growth lines. The radial ribbing, while exhibiting similar bifurcation and intercalation to that seen on *T. imbricata* sp. nov. and *T. nodulosa* Etheridge, is less prominent.

MATERIAL. Numerous specimens from the J. F. Walker Collection and many other sources in the British Museum (Natural History), British Geological Survey and the Sedgwick Museum, Cambridge.

Terebratulina nodulosa Etheridge

Pl. 5, fig. 16; Pl. 19, figs 3, 4; Pl. 21, figs 1–4.

1881 *Terebratulina nodulosa* Etheridge: 148; fig. 13.
1903 *Terebratulina nodulosa* Etheridge: Jukes-Browne & Hill: 204, 215, 224.

EMENDED DESCRIPTION. Circular to oval in outline with strong radiating ribs (14–18) orna-

mented by well-developed nodules. Short umbo truncated by large circular foramen. Average size about 9·5 mm in length, 8·6 mm wide and 2·4 mm thick.

NEOTYPE. B.G.S. specimen No. 117521; from the Totternhoe Stone, Burwell Rock; Burwell, Cambridgeshire (Pl. 21, figs 2–4). Herein selected.

REMARKS. Etheridge (1881) described two species of *Terebratulina* from the Cambridge area, one of which, *T. triangularis* (now *T. etheridgei*) has been discussed on p. 147; the other, *T. nodulosa*, was described from the Totternhoe Stone of Cherry Hinton. Unfortunately, the type specimen, which was represented in Etheridge's illustration (1881: fig. 13) is lost. A specimen subsequently thought to have been the holotype was found to be *T. triangularis* from the Cambridge Greensand; a neotype is therefore selected.

OCCURRENCE. The nodular ribs of *T. nodulosa* are distinctive amongst species of *Terebratulina*. Specimens are known from the Upper Albian at Hunstanton and from the Lower Chalk of Folkestone and Dover, and eight from the Lower Chalk, Bed V, of Lydden Spout, Folkestone (B25004). One in the collections of the B.G.S. (no. Hr.9030) came from the top of the *O. mantelliana* Band of Kennedy [= Tottenhoe Stone Horizon] from the Dover Pier borehole, at a depth of 202 ft. In addition *Terebratulina nodulosa* appears in the faunal list given by Jukes-Browne & Hill (1903: 40) from Bed 4 (Bed V of Price) in the Lower Chalk at Folkestone.

Terebratulina imbricata sp. nov.
Pl. 22

Terebratulina ornata (Roemer); auctt.
Terebratulina nodulosa Etheridge; auctt.

DIAGNOSIS. Oval to subcircular in outline. Umbo short, foramen small, circular. Ornament of about 18 coarse ribs, but up to 20 on some specimens. Growth lines imbricate. Rectimarginate. Average length 6·7 mm, width 5·8 mm, thickness 2·2 mm.

NAME. 'Overlapping like tiles'.

DESCRIPTION. This small *Terebratulina* is characterized by the frequent marginal ventral bifurcation and dorsal intercalation of its ribs, and by its lamellose growth-lines which produce an imbricate surface ornament. Additional ornament occurs as faint rounded papillae lying principally between the costellae (Pl. 22, figs 2–4). The rib nodules, so characteristic of many species of *Terebratulina*, occur faintly where weak growth lines cross the ribs, especially during early stages of growth and around the umbonal regions. No folding or sulcation of the valves occurred at any stage of growth, and the anterior commissure remains rectimarginate.

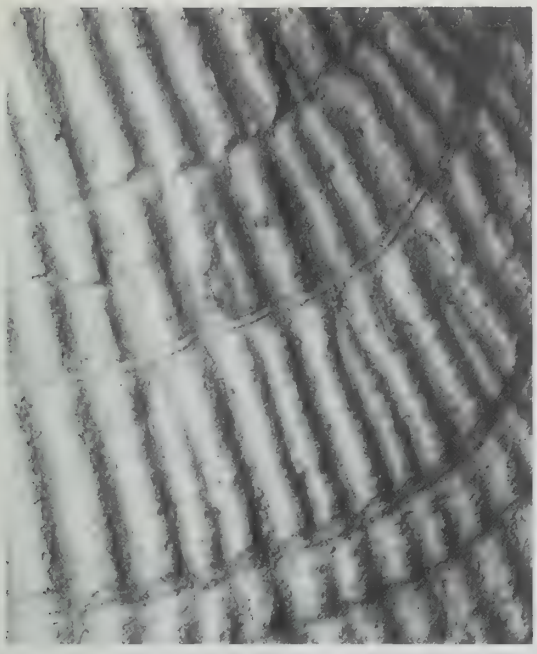
HOLOTYPE. Collection of C. W. & E. V. Wright, BB82196; Lower Pink Band (Bower & Farmery Bed V equivalent), Lower Chalk; Rifle Butts Pit, Market Weighton, Humberside (Pl. 22, figs 1–4).

PARATYPES. Three other specimens from the same collection, BB82197–9; and five specimens from the same horizon at Clapham's Limeworks, near Louth, Lincolnshire, in the collections of the B.G.S., Nos 99058–62.

PLATE 20

Figs 1–2 *Terebratulina protostriatula* sp. nov. Chalk Marl, Hamsey, E. Sussex. BB82416. Fig. 1, shell surface ornament on brachial valve. SEM × 30. Fig. 2, nodulose ornament from umbonal region. SEM × 40.

Figs 3–4 *Terebratulina striatula* (Mantell). Fig. 3, shell surface ornament of brachial valve of holotype now assigned to the Upper Chalk. B457, SEM × 35. See also Pl. 5, figs 7–9. Fig. 4, shell surface of the brachial valve of specimen from the Upper Chalk, *cortestudinarium* Zone, Wiltshire. The angular nature of the striae contrasts with those of *T. protostriatula* from the Lower Chalk. BB82417, SEM × 35.



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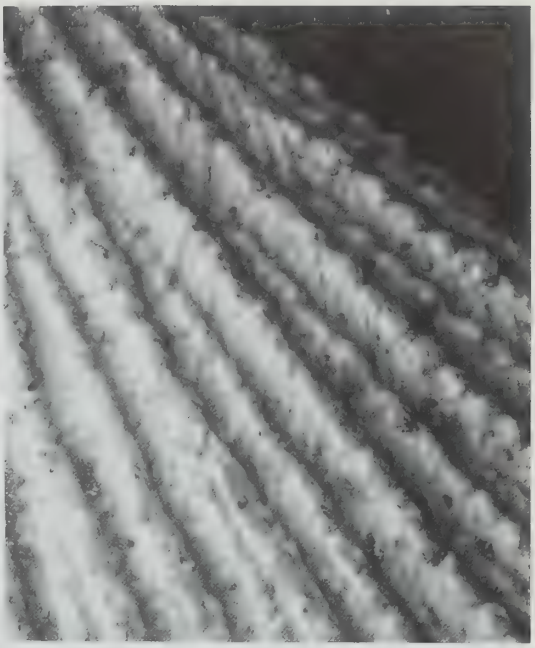

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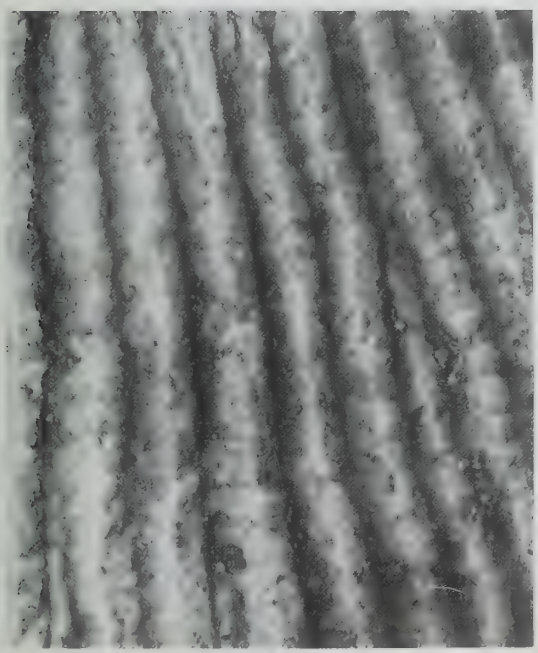

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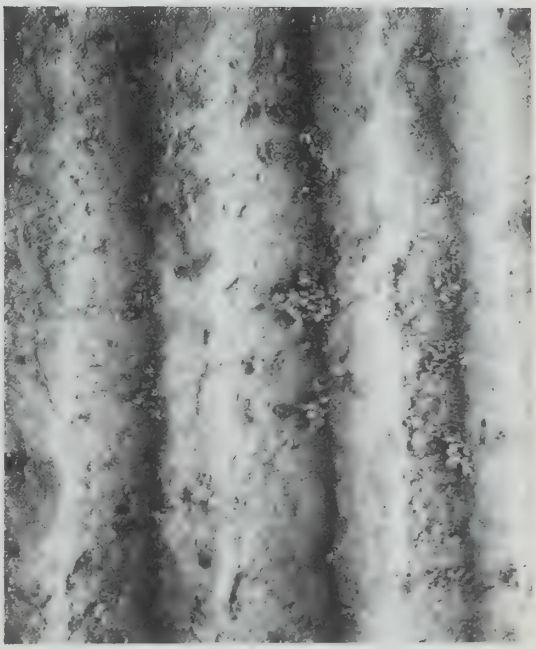

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Specimens have also been collected by K. Evans from the Lower Pink Band at Hubbard's Vale, near Louth, Lincolnshire.

REMARKS. As Bower & Farmery's collection was destroyed during World War II, the identification of the species they (Bower & Farmery 1910) called '*Terebratulina ornata*' in the Lower Pink Band remains unknown. *Terebratulina nodulosa* Etheridge, originally from the Totternhoe Stone, Cambridge, has more recently been collected from beds above the Totternhoe Stone, and Jukes-Browne & Hill (1903: 224) recorded it from the Totternhoe Stone and younger beds in Lincolnshire. *T. nodulosa* is thus the species most likely to have been the one called *T. ornata* Roemer by Bower Farmery, because their nodulose shell ornament is so similar; I believe that *T. imbricata* sp. nov. is a distinct species, which may prove stratigraphically important.

Terebratulina protostriatula sp. nov.
Pl. 5, figs 1–6, 13–15; Pl. 20, figs 1–2

Terebratulina striatula (Mantell); auctt.
1826 *Terebratulina striatula* J. de C. Sowerby: 69; pl. 536, figs 3, 4 (*non* Mantell).
1852 *Terebratulina striata, sensu* Wahlenberg; Davidson: pl. 2, figs 25, 27, 28.

DIAGNOSIS. Elongate-oval, uniplicate, evenly biconvex *Terebratulina*. Symphytium well exposed, foramen large, circular. Ornament of rounded bifurcating costellae.

NAME. 'Forerunner of *striatula*'.

DESCRIPTION. Frequent growth-lines interrupt the longitudinal costellae. In young and some well preserved adults the ornament is nodulose in the umbonal region of each valve. The umbo, though slightly produced, is more massive or less constricted than in species from the Middle and Upper Chalk.

Variation occurs in the degree of slight anterior sulcation, a tendency towards a more spatulate general outline, and in the density of costellation.

HOLOTYPE. Mantell Collection, B6038; from the Chalk of Hamsey, Sussex.

PARATYPES. One from the Lower Cenomanian of Wilmington, Devon, BB82261; 12 from the Chalk Marl, Dover, Kent, B29707; 1 from the Lower Chalk, Eastbourne, Sussex, B4804; 1 from Bluebell Hill, Burham, Kent, B9458; 2 from Peter's Quarry, Burham, Kent, B44805–6; 2 from the Glauconitic Marl of Warminster, Wiltshire, B54862–3; 5 from the Glauconitic Marl, St Lawrence, Isle of Wight, B75; 1 from the Lower Chalk of Newington's Chalk Pit, SE of Glynde railway station, BB862; 4 from the Lower Chalk of Balcombe Pit, Glynde, Sussex, BB43940–3; 5 from the lodge to Newtimber Place, Newtimber Church, Sussex, BB43965–9; 1 from the limeworks at Chinnor, Oxfordshire, B47302; 5 from the Upper Greensand of Deverill Hill, Dorset, B7003; 1 from the Upper Greensand, Ventnor, Isle of Wight, B10676; 6 from the Chalk Marl, Hamsey, Sussex, BB6038–43; 3 from the chalk above the Basement Bed, Punfield Cove, Swanage, BB76500–2; 15 from the Grey Chalk, Bed V (Price), Lydden Spout, Folkestone, Kent, B25003; 2 small individuals from the Cambridge Greensand, B7002; 3 from the Glauconitic Marl, Rocken End, Isle of Wight, BB76451–3; 1 from Bed 6 of Jukes-Browne (Lower Chalk), from a cutting in railway between Dover and Folkestone, BB82363; 8 from the Lower Chalk, Le Havre, France, B35181; 2 from Cap Blanc Nez, France, B700; 3 perfect examples from Cran d'Éscalles, Cap Blanc Nez, Boulonnais, France, BB82364–6.

PLATE 21

Figs 1–4 *Terebratulina nodulosa* Etheridge. Fig. 1, Middle Cenomanian, Flöteberg, Germany. BB82350, SEM × 12. Figs 2–4, Totternhoe Stone, Burwell, Cambridge. **Neotype** here selected, BGS coll. no. 117521. Fig. 2, SEM × 12. Figs 3–4, enlargements of shell surface to show nodular ornament. Fig. 3, SEM × 25. Fig. 4, SEM × 50.

Figs 5–6 *Terebratulina triangularis* Etheridge. Cambridge Greensand, Cambridge. BB82413. Fig. 5, SEM × 10. Fig. 6, enlargement of shell surface ornament, SEM × 30.

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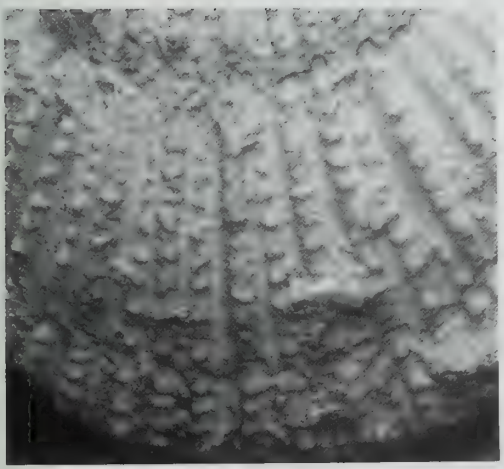

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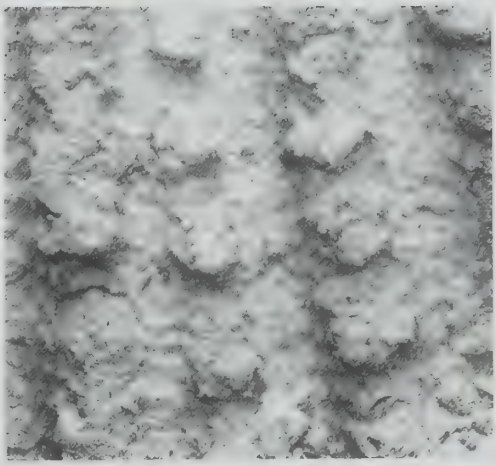

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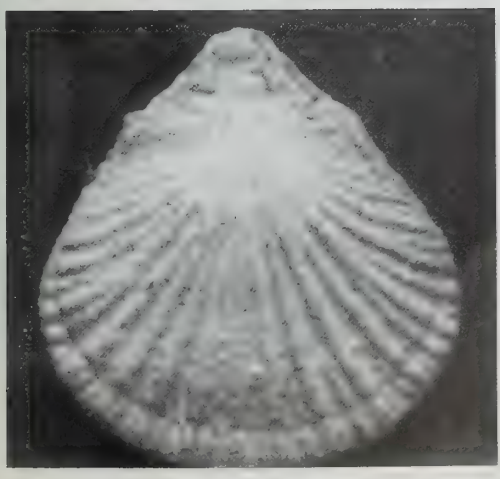

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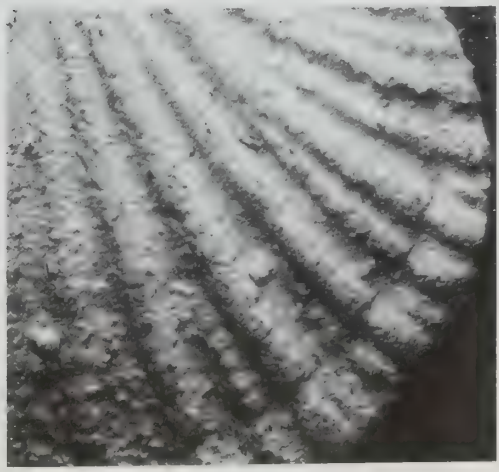

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REMARKS. This is the species which Mantell (1822) had in mind when he described a specimen from the Chalk Marl of Hamsey in Sussex. Unfortunately he figured (1822: pl. 25, figs 7, 8, 12) a specimen which, to judge from the adhering matrix and general morphological features, originated from the Upper Chalk. As no other specimens were involved at the time of description, Mantell's specimen (Pl. 5, figs 7–9; Pl. 20, fig. 3) must be regarded as the holotype of *Terebratulina striatula* (B457); it is 21·4 mm long, 17·4 mm wide, and 9·3 mm thick. It is larger than and differs in outline from any specimen I have examined from the Lower Chalk. In addition it has a marked ventral median sulcus extending from the umbonal region and becoming slightly deeper and wider anteriorly. The surface ornament of fine costellae is like that found on specimens of *Terebratulina* from the *Micraster cortestudinarium* Zone of the Coniacian from downland areas and other chalk exposures in both southeastern and southwestern England. Photomicrographs of *T. striatula* (Pl. 20, figs 3, 4) and *T. protostriatula* sp. nov. (Pl. 20, figs 1, 2) show clearly that the Upper Chalk species has longitudinal costellae which are transversely quadrate in section, while those of the Lower Chalk species are rounded. Mantell's specimen presumably originated from the Upper Chalk of Hamsey, and his name should therefore in future be restricted to specimens from the Upper Chalk.

The name *Terebratulina striatula* cannot therefore be applied to another *Terebratulina* species from the Lower Chalk. The present form is a species of *Terebratulina* occurring in the Coniacian of various localities in England, often quoted erroneously as *T. striata* (Wahlenberg). Wahlenberg's species, however, was originally described from the Upper Maastrichtian of Sweden; the original description is brief (Wahlenberg 1821: 61) and there is no illustration available. Specimens in the British Museum (Natural History), obtained by exchange from Sweden, are very large, 40–50 mm in length, and quite distinct from any species of *Terebratulina* from the British Upper Chalk.

Davidson (1852) used *Terebratulina striatula* in the broader interpretation of Sowerby (1829: 69), which included both Cretaceous and Tertiary forms, and applied it to a specimen collected from the London Clay of Sheppey, despite his contention that many Mesozoic and Tertiary species should be assigned to *T. striata* Wahlenberg. Elliott (1938) included *T. striatula* in the synonymy of his species *Terebratulina wardenensis*.

T. protostriatula sp. nov. differs from *T. auriculata* Roemer (1841), from the Hilsconglomerat of the Essen district in north Germany. Roemer's illustration (1841: pl. 7, fig. 9) shows a small, very flat uniplicate specimen with a slightly extended hinge line and a large circular foramen. The growth-lines are not very marked and the costellae appear somewhat coarser than those of any British Cenomanian specimens I have examined. Roemer's name has not been used for a specimen of *Terebratulina* since d'Orbigny (1847) used it in his classic work on the Cretaceous; furthermore, the exact horizon within the Hilsconglomerat of Essen is not known, the beds ranging from Neocomian to Cenomanian in age.

For these reasons I now erect *T. protostriatula*, rather than using Roemer's name *auriculata*, for the species formerly known under the erroneous name *Terebratulina striatula* Mantell and commonly found in the Lower Chalk of Britain and the European continent.

OTHER MATERIAL. Numerous specimens from the Lower Chalk of Britain and the Continent are in the British Museum (Natural History) and the British Geological Survey.

PLATE 22

Figs 1–4 *Terebratulina imbricata* sp. nov. Lower Pink Band, Rifle Butts Pit, Market Weighton, Humberside. **Holotype**, BB82196. Fig. 1, shell ornament of imbricate growth-lines and additional intercostal papillae. SEM × 15. Fig. 2, intercalation of costae and bifurcation. SEM × 35. Fig. 3, imbricate growth-lines at margin. SEM × 38. Fig. 4, small intercostal papillae. SEM × 45.

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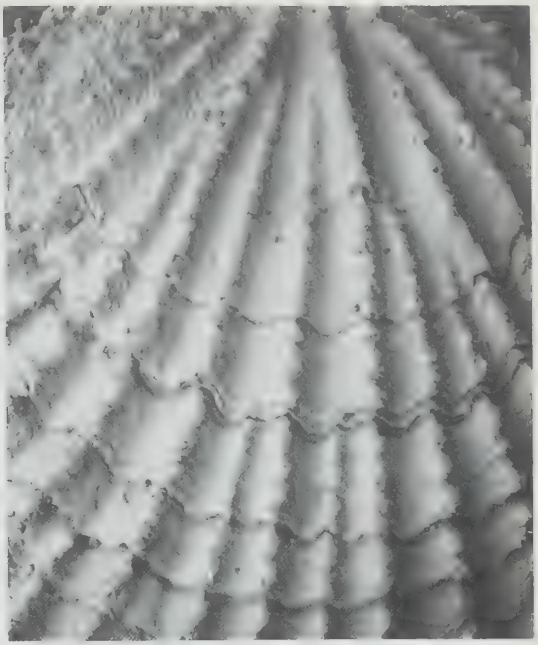

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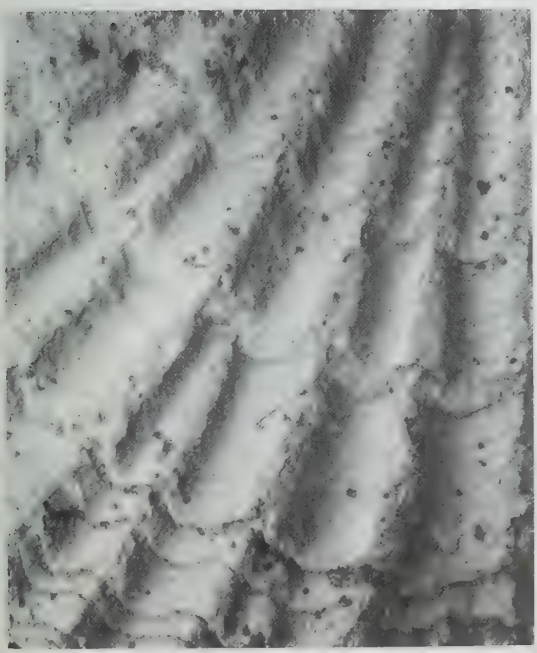

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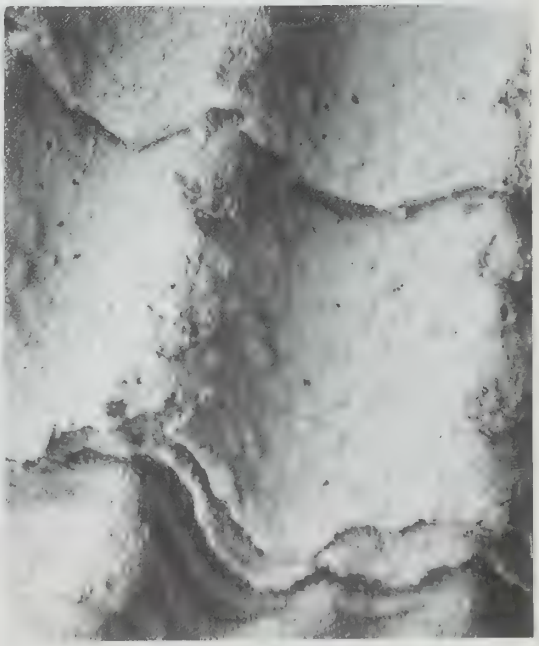

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Superfamily **ZEILLERIACEA** Allan, 1940

Family **ZEILLERIIDAE** Allan, 1940

Genus ***MODESTELLA*** Owen, *in* Casey 1961

Modestella geinitzi (Schloenbach)
Pl. 18, figs 17–22

1866*a* *Magas geintzi* Schloenbach: 575.
1866*b* *Magas geinitzi* Schloenbach; Schloenbach: pl. 2, figs 4–8.
1903 *Magas geinitzi* Schloenbach; Jukes-Browne & Hill: 67, 91.
1972 *Modestella* sp.; Popiel-Barczyk: 134; pl. 3, figs 1–3, 7a–c.

DESCRIPTION. Small zeilleriid brachiopod approximately 8 mm long, 8 mm wide and 6 mm thick. Maximum width at about shell mid-length. Pentagonal in outline with short umbo, sharp suberect beak, distinct beak-ridges and relatively large circular foramen. Conjunct deltidial plates exposed. The concave interarea is not extensive. Anterior commissure sulcate to sulco-carinate. The dorsal sulcus starts halfway down the valve and deepens slightly anteriorly. Two or three well developed step-like growth-lines occur anteriorly at about two-thirds the length of the shell.

HOLOTYPE. The whereabouts of Schloenbach's original specimen is unknown.

REMARKS. Schloenbach (1866*a*: 575) described, without figuring, the species as *Magas geinitzi* from the Cenomanian 'Grünsand von Quedlinburg' of north Germany, but later the same year (1866*b*: pl. 2, fig. 4–8) he figured an example from the same locality.

British examples have been quoted by British authors as *Magas geinitzi* Schloenbach, although differing from the German specimens in their slightly larger overall dimensions, the German specimens being approximately 6 mm long, 6 mm wide and about 4 mm in thickness.

Popiel-Barczyk (1972: 134) referred Polish examples of this species to *Modestella* sp., illustrating a series of transverse serial sections of a specimen from the Lower Cenomanian of Annopol, Poland. The geological range of the genus was thus extended from Lower Albian, from which it was first described, to Lower Cenomanian. No transverse serial sections were given with the original description (Owen, *in* Casey 1961) but were provided later (Owen 1963: 199–203) in a more comprehensive description of the genus. Popiel-Barczyk's (1972) serial sections show an even more complete series of the internal characters of this species.

Jukes-Browne & Hill (1903: 257) recorded the species as *Magas geinitzi* ? Schloenbach from the *A. mantelli* Zone of northwestern France and as *Magas geinitzi* Schloenbach from the Lower Chalk of Norfolk, Isle of Wight and west Sussex. Oddly enough, they do not quote it from Folkestone, where it occurs abundantly, nor does the species appear among the brachiopods listed from either the Lower or Middle Cenomanian of Folkestone by Kennedy (1969: 532–535). This is probably because some homoeomorphy exists between this species and *Capillithyris squamosa* (Mantell) (p. 142), which also occurs commonly at Folkestone.

MATERIAL. Numerous specimens in the British Museum (Natural History), including the following from the Chalk Marl of Hamsey, Sussex, BB3436–43; from the Lower Chalk of Folkestone, B25016, BB82214; from a similar horizon at Rougefort, Liques, Pas de Calais, B35200; and from the Greensand of Essen, north Germany, BB82213.

The species appears to be confined to localities in Britain and northern France with a marly

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PLATE 23

Figs 1–4 '*Argyrotheca*' *megatrema* (J. de C. Sowerby). Cambridge Greensand, Cambridge; species formerly assigned to *Argiope* by authors. Shell surface ornament resembles that of an immature *Terebratulina* sp. and supports the additional ornament of intercostal papillae seen in *T. imbricata* (pl. 22, fig. 4) from the Lower Pink Band of Yorkshire. BB6097, SEM × 22, × 16, × 50, × 100 respectively.

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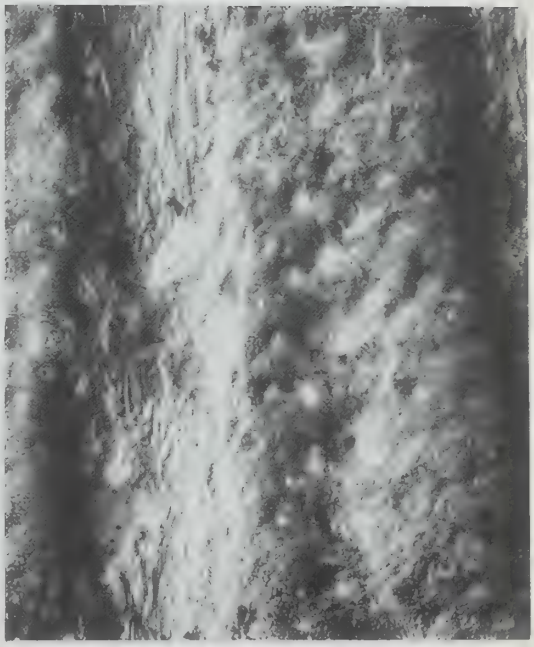

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limestone facies. The original occurrence in the Greensand of Quedlinburg and the specimens from the Annopol district of Poland may be exceptions to this preference, although little is known about the sediments from either of these two localities.

Family **MEGATHYRIDIDAE** Dall, 1870

Genus *ARGYROTHECA* Dall, 1900

'*Argyrotheca*' *megatrema* (J. de C. Sowerby)

Pl. 5, fig. 27; Pl. 23; Pl. 24

1836 *Terebratula megatrema* J. de C. Sowerby: 343; pl. 18, fig. 3.
1852 *Argiope megatrema* (J. de C. Sowerby) Davidson: 102; pl. 12, figs 31, 32, 34.
1852 *Argiope buchii* de Hagenow; Davidson: 102; pl. 12, fig. 33.

EMENDED DESCRIPTION. Small, biconvex, transversely oval terebratellid with short, almost straight, massive ventral umbo truncated by a large circular foramen. Well defined beak-ridges border a fairly extensive triangular ventral interarea. A disjunct delthyrium is poorly developed. Shell ornament consists of 16–18 strong radiating costae with few intercalations. Shell surface covered with raised papillae or nodules. Fine endopuncta are more readily observed on worn parts of the exterior and internally.

Anterior commissure rectimarginate to incipiently sulcate, but without evidence of a corresponding brachial fold.

INTERNAL STRUCTURES. *Pedicle valve.* There are neither supporting dental lamellae for the short massive hinge-teeth, nor is there any indication of a median septum.

Brachial valve. There is no differentiated cardinal process, but a myophore exists between the inner socket ridges. The broad fused hinge-plates, with massive rounded inner and outer socket ridges, form a shallow hinge-trough supported by a low, comparatively short, median septum extending anteriorly to support the wide descending branches of the brachial loop at about the mid-length of the valve.

TYPE SPECIMEN. J. de C. Sowerby (1836) originally described *Terebratula megatrema* from the Upper Greensand of Warminster, figuring a specimen (pl. 18, fig. 3) which is not in the Sowerby Collection at the British Museum (Natural History) because, like so many of the brachiopods figured in the same publication, it never formed part of his personal collection. Thus at present no type specimen is recognized.

REMARKS. Although never regarded as a common species from the Upper Greensand and Lower Chalk, '*Argyrotheca*' *megatrema* occurs more commonly in collections from the Cambridge Greensand. Fifty-five specimens collected by J. F. Walker from the Cambridge district can be added to the three in the Davidson Collection at the British Museum (Natural History); one (38073), from the Lower Chalk of Kent, was figured by Davidson (1852: pl. 12, fig. 33), having been given to him by S. P. Woodward.

On the same plate, Davidson (1852: pl. 12, fig. 37) reproduced von Hagenow's (1842) original figure of *Argiope bronni* from the Upper Chalk of north Germany, which he considered a synonym of *T. buchii* von Hagenow (1842). Both of these are regarded as generically and specifically distinct from *A. megatrema* (J. de C. Sowerby). *Argiope bronni* was cited by Popiel-Barczyk & Smirnova (1978) as type species for their new genus *Bronnothyris* from the Maastrichtian of north Germany and Poland, distinguished from *Argyrotheca* and all other

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PLATE 24

Figs 1–3 '*Argyrotheca*' *megatrema* (J. de C. Sowerby). Cambridge Greensand, Cambridge. B5247. Fig. 1, internal structure showing broad but broken brachial loop, large hinge-teeth and extensive hinge-line. SEM × 15. Fig. 2, enlargement to show broken supporting septal pillar and hinge-trough with endopuncta. SEM × 34. Fig. 3, further enlarged to show shallow but broad hinge-trough, thickened inner socket-ridges and endopuncta. SEM × 65.

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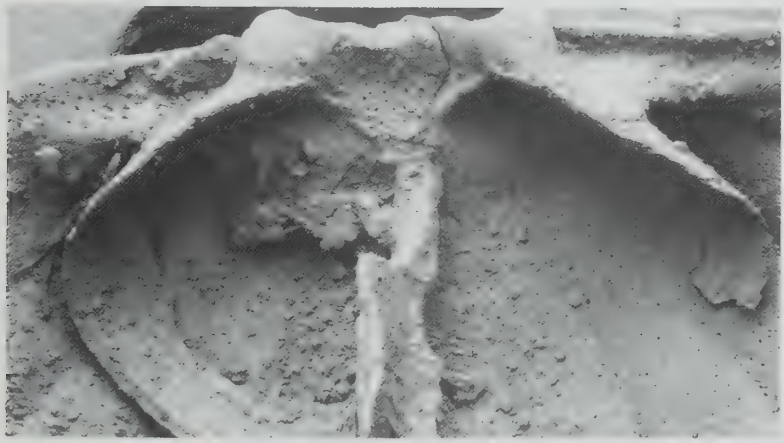

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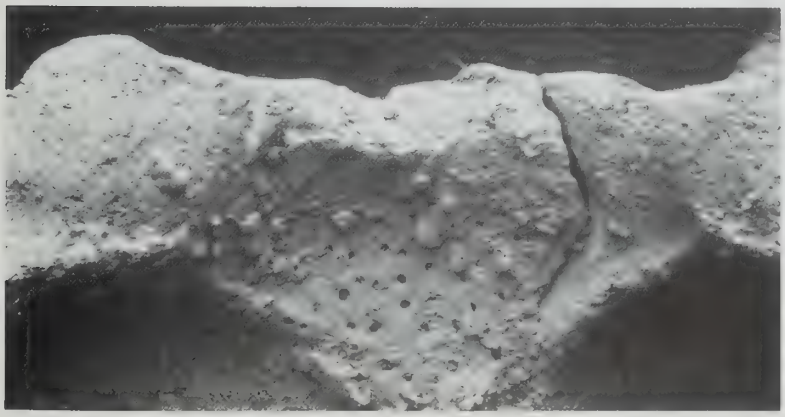


3

megathyrid genera by the presence of rudimentary or incipient ascending branches of the brachial loop. It can be further distinguished from '*Argyrotheca*' *megatrema* (J. de C. Sowerby) by its extended hinge-line, fewer and non-bifurcating costae, more triangular outline and the absence of papillae on the shell exterior.

The presence or absence of these papillae in the Megathyrididae is thought by Nekvasilova (1983) to be the result of some secondary condition, such as mode of preservation. Her explanation is that the papillae are calcite infillings of large puncta protruding above the shell surface and forming a papillate pseudosculpture. But why should this condition affect species within the Megathyrididae and leave other species of punctate genera unaffected? It is more likely that this is part of the primary ornamentation.

Family **DALLINIDAE** Beecher, 1893

Subfamily **Uncertain**

Genus ***ARENACIARCULA*** Elliott, 1959

Arenaciarcula beaumonti (d'Archiac)
Pl. 17, figs 7–9, 28–30

1847 *Terebratula Beaumonti* d'Archiac: 331; pl. 21, figs 12–14.
1867 *Terebratula* (?) *Beaumonti* d'Archiac; Schloenbach: 461; pl. 22, figs 3–5.
1869 *Trigonosemus kiprijanovi* Hofman: 25; pl. 5, figs 18–21.
1871 *Terebratula orbicularis* Sow.; Quenstedt: 293; pl. 45, figs 63–69.
1874 *Terebratella Beaumonti* (d'Archiac) Zareczny: 177; pl. 2, fig. 3.
1916 *Terebratella Beaumonti* (d'Archiac); Ravn: 22; pl. 4, fig. 8.
1969 *Terebratella beaumonti* (d'Archiac); Panow: 593; pl. 112, fig. 5.
1972 *Oblongarcula beaumonti* (d'Archiac) Popiel-Barczyk: 127; pl. 1, figs 1–5; pl. 4, fig. 3.
1977 *Arenaciarcula beaumonti* (d'Archiac) Owen: 236; pl. 2, figs 7a–c.

Remarks. This species was reviewed by Owen (1977) and the geographical distribution was given as Britain, Belgium, Poland, Germany, Denmark and the U.S.S.R., to which can now be added southern France. The specimen figured (Pl. 17, figs 7–9), from the Cenomanian near Nice, is an especially large variant, being larger than any of the specimens collected from Belgium or Britain, but closely resembling the specimen figured by Panow (1969) from the Krakow district of Poland.

Family **TEREBRATELLIDAE** King, 1850

Subfamily **TRIGONOSEMINAE** Elliott, 1965

Genus ***DERETA*** Elliott, 1959

Type species. *Terebratella pectita* (J. Sowerby, 1816).

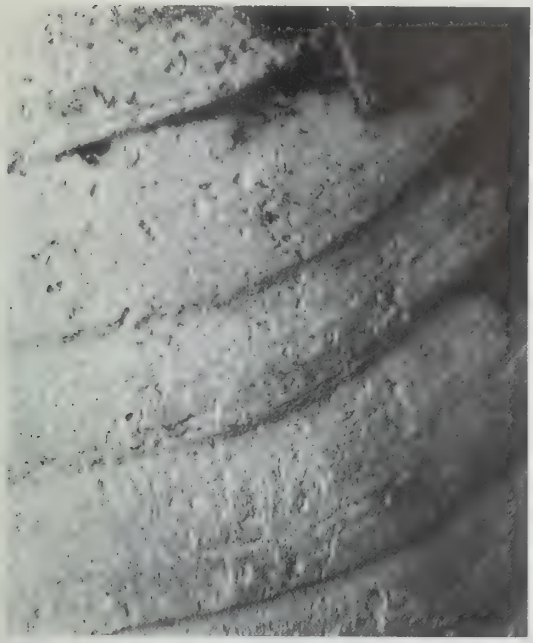
Dereta pectita (J. Sowerby)
Figs 29–30; Pl. 17, figs 10–15

1816 *Terebratula pectita* J. Sowerby: 83; pl. 138, fig. 1.
1819 *Terebratula pectita* Sow.; Lamarck: 255.
1822 *Terebratella pectita* (Sow.) Brongniart, *in* Brongniart & Cuvier: pl. 9, fig. 3.
1838 *Terebratula pectita* Sow.; von Buch: 168; pl. 16, fig. 12.

PLATE 25

Figs 1–2 *Ovatathyris potternensis* sp. nov. Glauconitic Marl, Potterne, Wiltshire. BB82149. Fig. 1, shell surface. SEM × 25. Fig. 2, shell margin showing immature remnants of spinules. SEM × 25.

Figs 3–4 *Ovatathyris ovata* (J. Sowerby). Cenomanian, Warminster, Wiltshire. Fig. 3, shell surface showing arrangement of spinules along margin. BB6012, SEM × 30. Fig. 4, surface of similar specimen showing spinules on brachial valve arranged in pairs. BB6009, SEM × 25.



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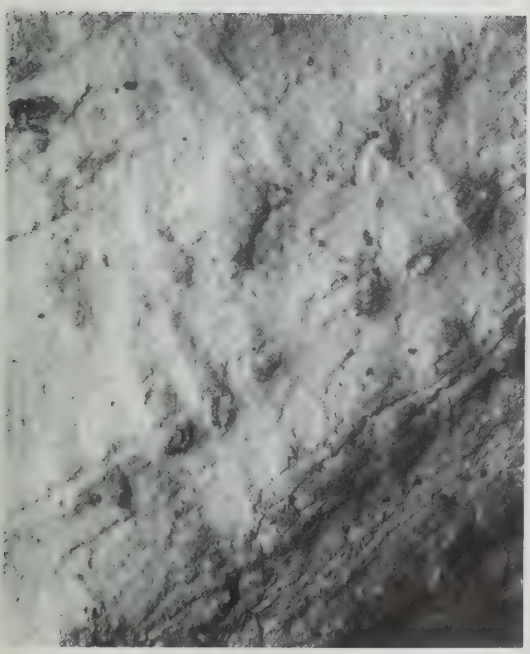

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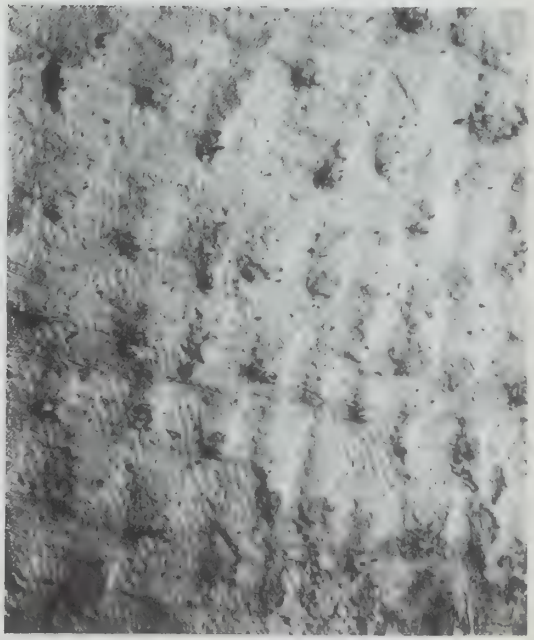

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1847 *Terebratella pectita* (Sow.); d'Orbigny: 120; pl. 517, figs 16–20.
1852 *Terebratella pectita* (Sow.); Davidson: 26; pl. 3, figs 29–33.
1871 *Terebratula pectita* Sow.; Quenstedt: 267; pl. 44, figs 104–5.
1959 *Dereta pectita* (J. Sowerby) Elliott: 147.
1965 *Dereta pectita* (J. Sowerby); Elliott: H853, fig. 736, 2a–c.
1977 *Dereta pectita* (J. Sowerby); Owen: 246; pl. 1, figs 8a–c.

HOLOTYPE. Sowerby Collection, B61622; from the Upper Greensand of Horningsham, Wiltshire. Figured J. Sowerby (1816: pl. 138, fig. 1). Length 19·9 mm; width 20·0 mm; thickness 14·0 mm.

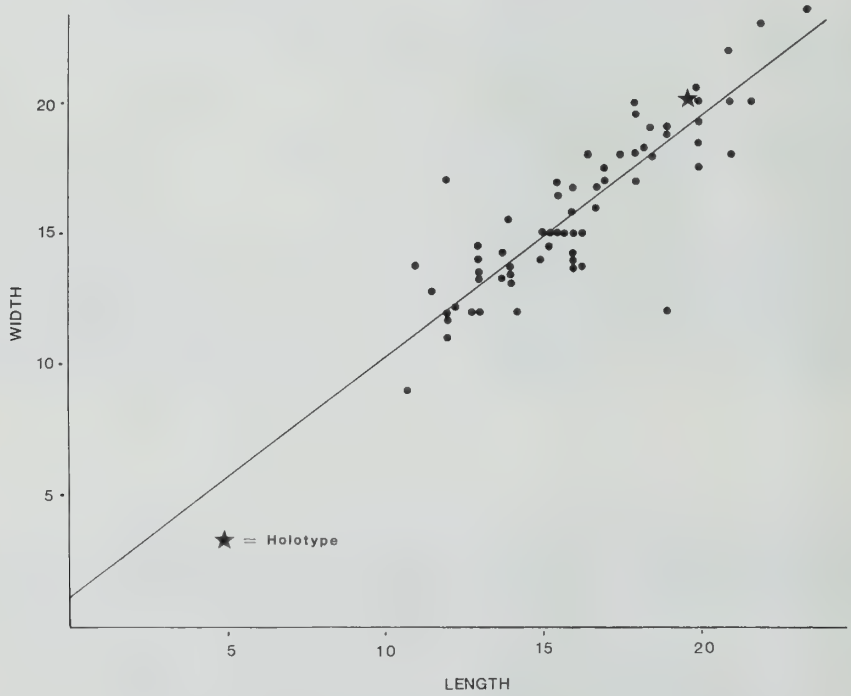

Fig. 29 Length × width graph and regression line for 65 specimens of *Dereta pectita* (J. Sowerby) from SW England.

REMARKS. This species was redescribed, with additional data from transverse serial sections, by Owen (1977); he mentioned (1977: 248) a variant from the Upper Albian, *dispar* Zone of Punfield Cove near Swanage, Dorset. It is redescribed below as *Dereta pectita ballardensis* subsp. nov.

D. pectita pectita (J. Sowerby) can be distinguished from the new subspecies by its evenly subcircular outline, equal biconvexity of valves, marked but regularly spaced growth-lines and comparatively fine costation. It has a more clearly defined triangular interarea and a slightly wider hinge-line.

PLATE 26

Figs 1–4 *Arcuatothyris arcuata* (Roemer). Chalk Marl, Folkestone, Kent. BB82352. Fig. 1, shell surface ornament of spinules showing indiscriminate arrangement and direction. SEM × 10. Fig. 2, area of accelerated growth between two growth-lines devoid of mature spinules. SEM × 25. Fig. 3, shell surface ornament showing interdigitation of spinules and relative length. SEM × 30. Fig. 4, ornament and growing edge of shell to show shortening of spinules. SEM × 50.

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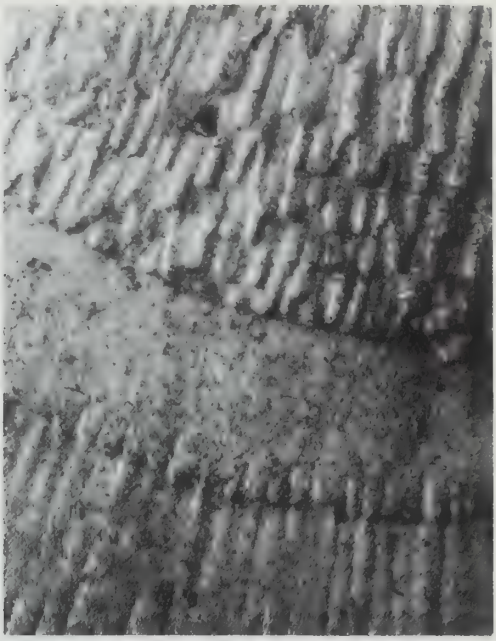

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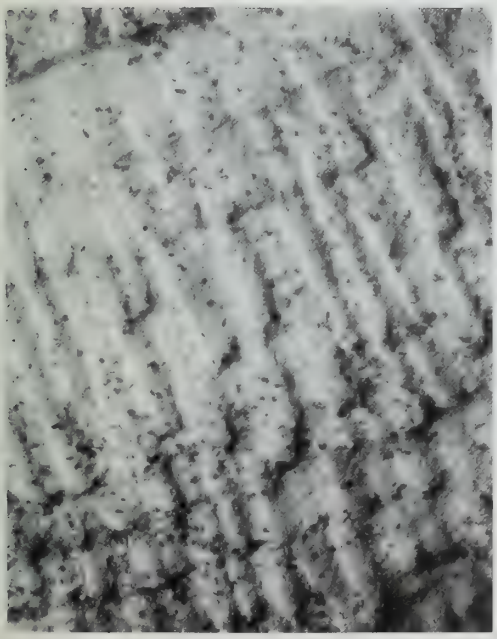

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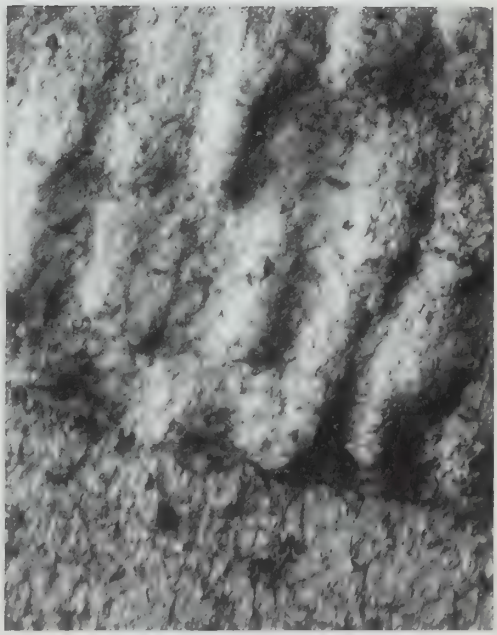

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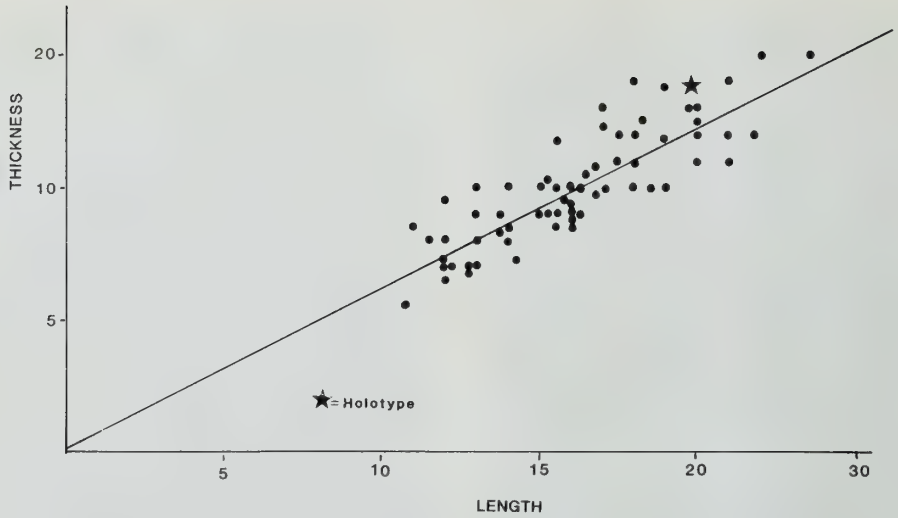

Fig. 30 Length × thickness graph and regression line for 65 specimens of *Dereta pectita* (J. Sowerby) from SW England.

Dereta pectita ballardensis subsp. nov.
Pl. 17, figs 16–18

NAME. 'From Ballard Point'.

DESCRIPTION. Subquadrate in outline, this subspecies is distinguished by its coarse costae and very prominent growth-lines. The umbo is massive and the beak erect to slightly incurved. The symphytium is not exposed. The beak-ridges are obscured by the heavy ornament. The ventral interarea is short and poorly defined. The anterior commissure is rectimarginate to incipiently ligate, a faint sulcus in the ventral valve being opposed by a similarly faint sulcus in the anterior part of the dorsal valve.

HOLOTYPE. BB82098; from the Upper Albian, *dispar* Zone of Ballard Point, near Punfield Cove, Swanage Bay, Dorset (Pl. 17, figs 16–18).

OTHER MATERIAL. Specimens in the British Museum (Natural History): from Lower Cenomanian, Melcombe Bingham, B25288; from Horningsham, B61622–3; and from the Warminster district BB4199, B25264. From the Upper Albian of Punfield Cove, Dorset, BB82099–105 (George Bate Colln).

Specimens in the Sedgwick Museum, Cambridge: from Punfield Cove, B7304; from Dunscombe, Devon, B7291–3; from Pinhay Cliff, B7502–8.

A unique specimen in the J. F. Walker Collection, B25289, was found in the Upper Greensand (basal bed) in an old orchard at Chelborough, Evershot, Dorset. It is somewhat worn but probably belongs to *D. pectita ballardensis*.

PLATE 27

Figs 1–4 *Capillithyris squamosa* (Mantell). Chalk Marl, Folkestone, Kent. BB82351. Figs 1, 2, surface showing 'capillate' ornament. SEM × 15, × 25 respectively. Figs 3, 4, views of a growth edge to show intercapillary cuspidation of the ornament of concentric growth-lines. SEM × 200, × 420 respectively.

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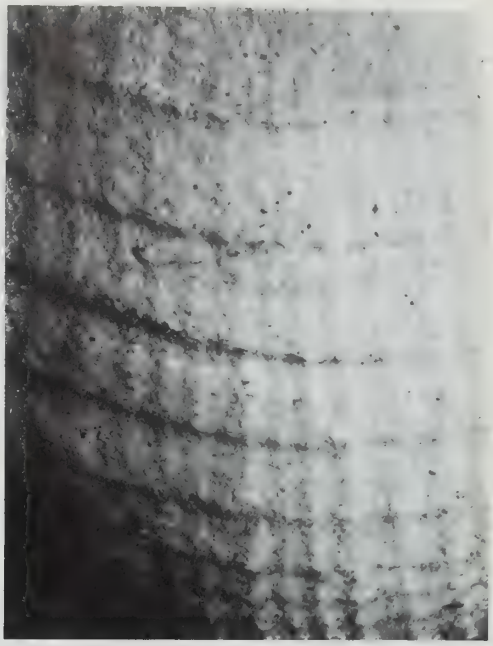

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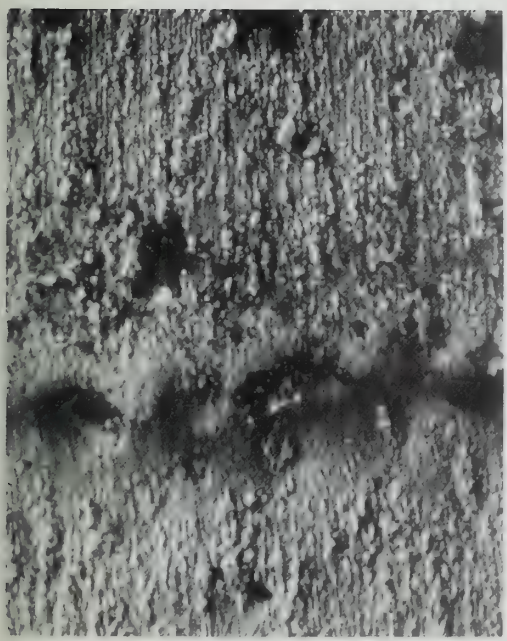

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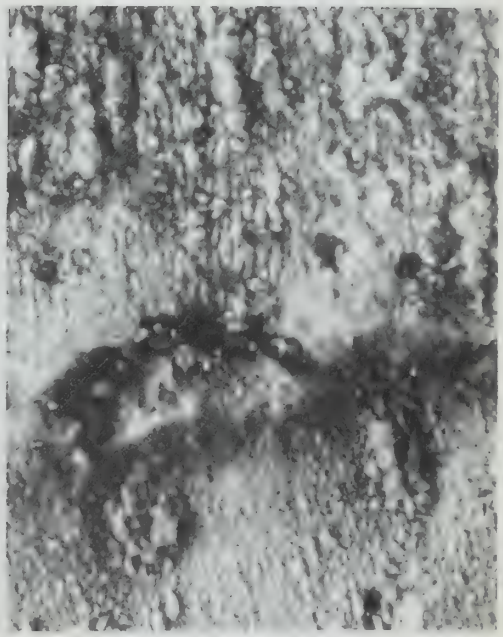

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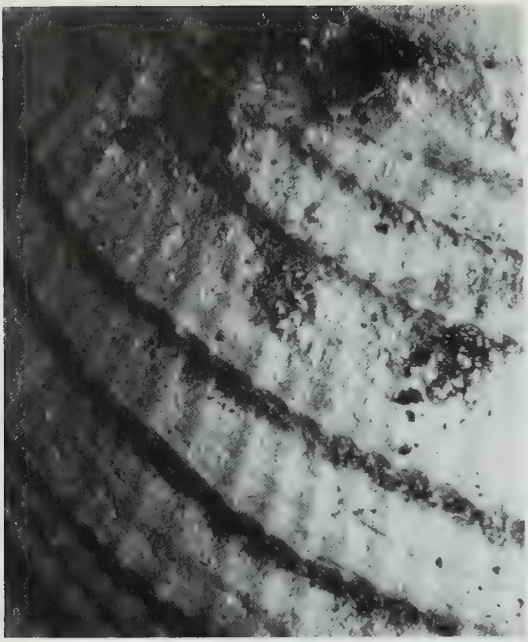

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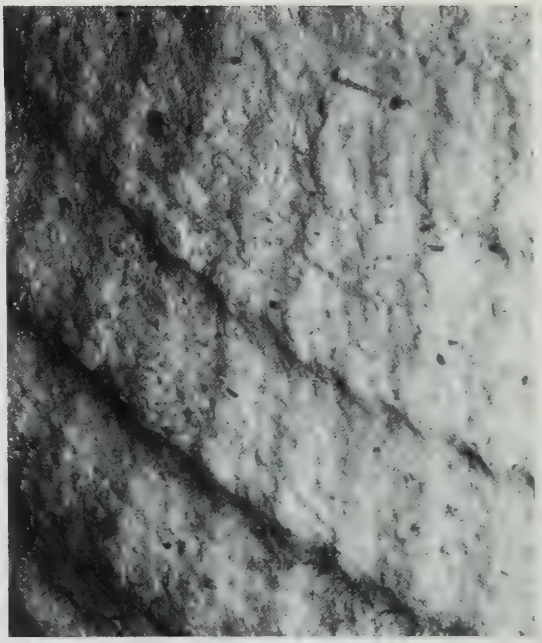

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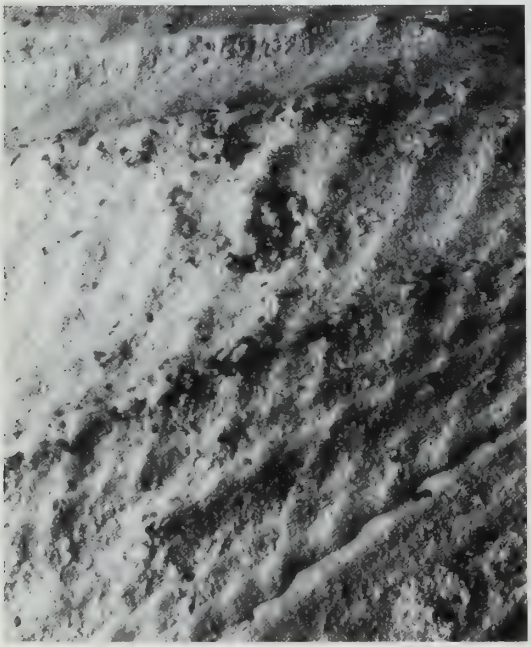

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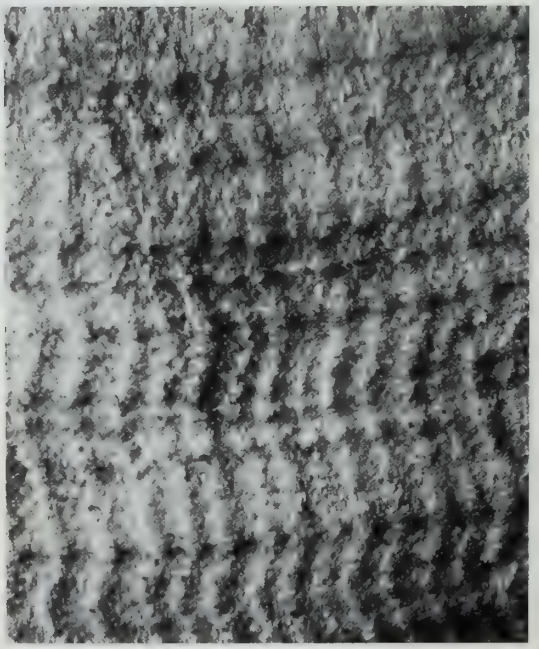

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Dereta incerta (Davidson)
Pl. 17, figs 25–27

1852 *Trigonosemus incerta* Davidson: 31; pl. 4, figs 5a–c.
1871 *Terebratella incerta* (Davidson) Quenstedt: 268; pl. 44, fig. 106.

EMENDED DESCRIPTION. Small species of *Dereta*. Average dimensions: length 8·4 mm; width 8·0 mm and thickness 5·4 mm. Hinge-line straight, ventral interarea broad, triangular; symphytium well exposed. Foramen circular, comparatively large. 28 to 30 rounded costellae with intercalations and marginal bifurcation. One to two well-marked growth-lines.

HOLOTYPE. Davidson Collection, BB82145; from the Glauconitic Marl, Chardstock, Devon. Figd Davidson 1852: pl. 4, fig. 5a–c.

REMARKS. The only published records are those of Davidson (1852) and Quenstedt (1871), but specimens have been found in Sussex by C. T. Gaster and in Dorset by W. J. Kennedy. In addition three possible specimens were collected from Bed B, White Cliff, Devon, and two from the same horizon at Little Beach, Beer Head, Devon by T. Grimsdale, B53190, B53191, B53192 respectively. These appear to be somewhat broader than the type specimen and could be dwarf forms of *D. pectita*. Two specimens slightly larger than the type specimen and with coarser costae were collected by C. W. & E. V. Wright from Downlands Beach, Devon (BB59325) and the Glauconitic Marl of Compton Bay, Isle of Wight (BB59317).

In the Meyer Collection in the Sedgwick Museum, Cambridge there are five specimens, two from Dunscombe from Meyer's Beds 10–12, B7308–9, and three from Bed 13 at White Nothe, Dorset, B20677–9.

The species is assigned here to *Dereta* entirely in consideration of its external morphology, as nothing is known about the internal structures. Some of the specimens recorded here as belonging to this species may, after further work, require reassignment.

Records of *Dereta incerta* show that most specimens were collected from a more highly calcareous or chalky lithology than that in which *D. pectita* is found, which may account for its wider distribution.

Superfamily **THECIDEACEA** Gray, 1840

Family **THECIDEIDAE** Gray, 1840

Subfamily **THECIDEINAE** Gray, 1840

Genus ***THECIDIOPSIS*** Oehlert, 1887

Thecidiopsis essensis (Roemer)
Pl. 5, figs 18–19

1837 *Thecidea digitata* Sowerby; Bronn: 664; pl. 30, fig. 4.
1840 *Thecidea essensis* Roemer: 36 (cit. Bronn 1837: pl. 30, fig. 4).
1854 *Thecidea digitata* (= *T. essensis* Roem.); Roemer: 136.
1959 *Thecidiopsis* (*Thecidiopsis*) *essensis* (Roemer) Backhaus: 50; pl. 4, fig. 8–9; pl. 5, fig. 1.

REMARKS. In his original description of *Thecidea essensis*, Roemer (1840: 36) cited the illustration by Bronn (1837: pl. 30, fig. 4) which, although poor by present-day standards, is sufficiently distinctive to allow differentiation of this species from other forms within the Cretaceous. The shell is transversely oval in outline. The brachial valve is approximately 10–12 mm long and between 12 and 14 mm wide. From the small collection of single valves and other material, it is possible to estimate that complete adult pedicle valves would be about 16 mm long and wide.

PLATE 28

Figs 1–4 *Capillithyris disparilis* (d'Orbigny). Cenomanian, Rouen, France. B35081. Figs 1, 2, cuspidation of capillate ornament similar to that seen in *C. squamosa*. SEM × 35, × 40 respectively. Figs 3, 4, posterior lateral and anterior lateral views, showing zigzag capillae noted in this species only and often situated marginally. SEM × 20, × 15 respectively.

The thickness varies according to the amount of secondary shell material deposited in older individuals, but averages 6–9 mm. It has a broad extensive triangular interarea and high pseudodeltidium.

An average of 8–10 descending branches of the brachial apparatus are separated by thin septae extending posteriorly from the shell margin.

A nearly perfect example of this species was figured by Backhaus (1959: pl. 4, figs 8, 9; pl. 5, fig. 1) from the Middle Cenomanian, Essen Greensand, north Germany. Another Essen Greensand specimen is here figured (Pl. 5, figs 18, 19) from the Davidson Collection, B5190.

Thecidiopsis essensis can be distinguished from the Hauterivian species *T. tetragona* and the Maastrichtian species *T. digitata* by its constantly broad oval outline, acutely triangular and extensive ventral interarea and short septum within the umbo of the pedicle valve. It has more numerous and more parallel branches to its brachial apparatus than *T. digitata*, which it most closely resembles, or than *T. tetragona* in which the branches are more lobate.

T. essensis has not been recorded from any horizon within the Cretaceous of Great Britain. A specimen described, but not figured, by d'Archiac (1847: 350) from the Tourtia of Belgium as *Thecidea digitata* Sowerby is probably *T. essensis* (Roemer).

Nekvasilova (1966: pl. 1, figs 1–6; 1974*b*: pl. 2, figs 3–6) described specimens from the Lower Cretaceous of Stramberk, Czechoslovakia, as *Thecidea* cf. *tetragona* (Roemer); they have the broad lobate brachial apparatus typical of *T. tetragona*, but bear some resemblance to *T. essensis* in the width of valves and in the number and arrangement of the branches of the brachial apparatus.

Faunal distribution

The distribution of brachiopod species of Boreal and Tethyan origin has been the subject of much discussion since Ager (1971), Middlemiss (1975) and Owen (*in* Dieni, Middlemiss & Owen 1973) demonstrated the cosmopolitan nature of some of the forms previously considered to have been confined to special ecological provinces. The Lower Chalk provides a good example, amongst many, of faunal groups thought to have originated in these two major realms.

The adaptability of brachiopods to changes within the environment makes delimiting exact ecosystems within such a community a very difficult task. It is fortunate, therefore, that the universal transgressive Cenomanian sea provided relatively stable conditions, with few changes in depth, so the resulting facies are limited. Ager (1965: 145) stressed the point that this stage within the Mesozoic probably provides the best example of a stable, comparatively shallow-water environment.

Within the broadly-defined Cenomanian are deposits which indicate areas of comparatively deeper water or quieter conditions, which support their own peculiar brachiopod faunas. In such places we see faunas somewhat analogous to Ager's 'Alpine Group', but having closer links with the overall fauna than the isolated 'Alpine Group' of species maintained with their contemporaneous adjacent faunas.

In 1978 I pointed out, in a general review of brachiopod species within the Cenomanian of northwestern and central Europe, that each ecological group within its own particular lithological unit appears to contain a fauna with a characteristic or dominant association together with some wider-ranging species which tend to fall into two groups; one characterized by rhynchonellids and costate terebratellids and the other by terebratulids and smooth terebratellids. The present study supports this view and I believe that these groups can be traced across Europe into north Germany and southern France while retaining their specific constitution. In so doing I have taken into consideration lithological and major geographical differences. For instance, in southeastern France, at Drap, near Nice, a collection of brachiopods has been made from highly glauconitic sandy limestone and from more argillaceous deposits nearby. The species from the glauconitic beds consists of large biplicate Terebratulidae similar in general form to *Moutonithyris dutempleana* (d'Orbigny) from similarly highly glauconitic deposits in Britain and northern France, while the fauna in the more argillaceous deposits is of smooth

Terebratulidae and small Rhynchonellidae—an assemblage like the one which characterizes the more marly beds within the Cenomanian of the Weald.

In Britain certain patterns can be recognized. In the south, particularly in the coarse sandy facies of the more western outcrops at Wilmington and Warminster, there is a fauna showing some characteristics of the two main lithologically controlled assemblages. I consider these to be marginal to their normal faunal distributions. Genera such as *Orbirhynchia*, *Grasirhynchia* and *Terebratulina* are found with acutely plicate Terebratulidae, such as *Boubeithyris diploplicata* and coarsely costate Cyclothyridinae, and the Terebratellidae *Dereta* and *Terebrirostra*. In addition, species such as the small ornate *Arcuatothyris arcuata* (Roemer) and *Capillithyris squamosa* (Mantell) are commonly found in the chalk facies of the Lower Chalk Basement Beds in Wiltshire and Dorset or the Craie de Rouen, where they occur with smooth, strongly biconvex Terebratulidae such as *Concinnithyris obesa* (J. Sowerby). *A. arcuata* and *C. squamosa* appear to be tolerant species, the former occurring also in the glauconitic limestones of north Germany and on the Normandy coast; the latter, along with *C. disparilis*, in the Chalk Basement Beds and Craie de Rouen and also in the Chalk Marl and marly facies of Kent and Sussex. *C. disparilis* is found again with the other two species in sandy facies of Bed C at Humble Point and at The Pinnacles, south Devon.

Grasirhynchia grasiana (d'Orbigny) appears to have adapted to coarse sandy glauconitic limestones, as well as to more finely marly deposits of the Middle Cenomanian of the Weald, Isle of Wight, Wiltshire, Dorset and Devon. It is also found widely in western and northern France, rarely in the hard marly beds of Brochterbeck, Tecklenberg, north Germany, and in Poland.

Summarizing, I consider that the Cenomanian transgressive sea extended from eastern Europe across Poland, Czechoslovakia, north Germany, Belgium, France and Britain, and that within this region there were areas of unusual environments. Further studies of these areas and their brachiopod faunas may shed light on the differences between these environments, and on the distributional parameters of the brachiopods.

It is possible to draw a broad comparison between the faunal composition of assemblages from Essen, north Germany, the Arnager Greensand of Bornholm, Denmark, the Tourtia of Belgium and the more argillaceous Cenomanian Sands of Wilmington, south Devon. Each of these areas appears to represent an individual facies containing elements of both the marly bed faunas and the harder, coarse sandy bed faunal elements discussed previously.

The more compact marly chalks and marls which occur within the same area seem to have supported a fauna living on a softer substrate and perhaps in deeper water. This is reflected in the composition of the assemblages which are characterized by smooth-shelled terebratulids and finer costate rhynchonellids. The absence of any costate terebratellids is also characteristic of quieter and deeper conditions.

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